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TRANSACTIONS

OF THE

AMERICAN ENTOMOLOGICAL SOCIETY

VOLUME LXXVII

THE LYCIDAE OF THE UNITED STATES AND CANADA. III. THE TRIBE PLATERODINI (IN PART) (COLEOPTERA)

BY JOHN WAGENER GREEN

Easton, Pennsylvania

(Plates I and II)

The Tribe *Platerodini*, as here understood, comprises all those elongate subparallel *Lycinae* having the front short and deflexed, with the mouth nearly vertical; the legs and antennae only feebly compressed; the second antennal joint small but conspicuous, neither strongly transverse nor partly concealed in the apex of the first joint; the antennal pubescence inclined, not prostrate, frequently erect and bristling in the male; the anterior thoracic spiracles not prominently tubulate; and the anterior coxae nearly or quite contiguous.

The preceding definition includes, in addition to *Plateros*, all the Nearctic genera heretofore assigned to the tribe Dictyopterini.[1] The two divisions are maintained, however, in modified form as subtribal groups. The first of these, the Dictyopteri, forms a natural link with the preceding tribe, the Lygistopterini, both groups having similarly tubulate male genitalia and a pronotal sculpture of the same general plan. The similarity of the pronotal sculpture may be better visualized by assuming the obsolescence of the

[1] Junk Col. Cat., pars 128, 1933, p. 35.

longitudinal carinae in *Dictyopterus,* leaving only a medially broadened central channel and an oblique carina each side, and reproducing quite closely the formation characteristic of lygistopterid genera.

Key to the Nearctic Subtribes and Genera

1. Pronotum with two more or less distinct longitudinal carinae inclosing a central cell; lateral lobes of aedeagus forming a tubulate sheath almost entirely enveloping the median lobe .....subtribe **Dictyopteri** 2
   Pronotum with a single longitudinal carina, this either entire, apical, or wanting; lateral lobes of aedeagus, when present, not enveloping the median lobe, the latter fully exposed beneath .....subtribe **Platerodi** 4
2. Longitudinal carinae of pronotum entire, confluent at base and at apex and inclosing a central rhombic cell .....**Dictyopterus** Mulsant
   Longitudinal carinae of pronotum not entire, the central cell not rhombic 3
3. Front normally deflexed; antennal sockets approximate ...**Eros** Newman
   Front acutely elevated transversely between antennal sockets, the latter rather widely separated .....**Platycis** Thomson
4. Longitudinal carina of pronotum entire .....**Lopheros** Leconte
   Longitudinal carina of pronotum apical or wanting 5
5. Outer discal costae of elytra strongly elevated, the first, or first and second, subobsolete; pronotum with a usually distinct oblique carina each side joining the lateral margin near basal fourth; lateral lobes of aedeagus sharply acuminate .....**Eropterus** new genus
   Discal costae of elytra similar throughout; pronotum without lateral carinae; lateral lobes of aedeagus, when present, not sharply acuminate 6
6. Antennae short and rather stout, less than half as long as the body in the male, the median joints subquadrate; size small, less than 4 mm. in length; aedeagus with lateral lobes .....**Pseudoplateros** new genus
   Antennae longer and slender, more than half as long as the body in the male, the median joints elongate; size larger, usually over 4 mm. in length; aedeagus without lateral lobes .....**Plateros** Bourgeois

NEOCELETES.—The type of *Neoceletes crateracollis* Leng and Shoemaker was examined at the National Museum through the courtesy of Mr. H. S. Barber, who had discovered that it is in reality a curiously deformed specimen of a species of *Plateros. Neoceletes* therefore is suppressed as a synonym of *Plateros.* Further discussion of *Plateros* is omitted from this paper and will be presented in a final installment of the series.

DICTYOPTERUS Mulsant

1838. *Dictyopterus* Mulsant, Ann. Soc. Agr. Lyon, 1, p. 180.

Form elongate, subparallel, very little wider posteriorly. Antennae simple, approximate at base; in the male slender and nearly filiform, over half as long as the body, second and third joints small, their combined length subequal to fourth, third longer than second, apical angles of following joints not produced; in the female shorter and stouter, somewhat compressed. Antennal prominence strongly elevated, divided by a longitudinal impression; eyes protuberant; front short before the eyes, strongly deflexed, mouth nearly vertical; mandibles stout, arcuate, more strongly bent at middle, overlapping when closed, their tips not recurved; clypeus free, transverse. Palpi similar in the sexes, not dilated, the maxillary gradually wider apically, terminal joint not compressed except at tip; terminal joint of labial palpi much wider than preceding joint, compressed, broadly triangular, apex strongly oblique and longer than inner side.

Pronotum small, subpentagonal, one-half to three-fourths wider than long, widest at base, anterior angles usually broadly rounded, lateral margins thence subparallel to basal third, thence diverging to the acute and laterally prominent posterior angles, base transverse; base, apex, and sides of pronotum reflexed, the sides more broadly, margins scarcely thickened. Disk with two entire longitudinal carinae confluent at base and at apex and inclosing a central rhombic cell, each side divided by an oblique carina extending from the mid-angle of the rhombic cell to the lateral margin at the reentrant angle near basal third (Pl. I, fig. 1).

Elytra about six times as long as pronotum and conjointly at apical fifth one-half wider to nearly twice as wide; each with three or four distinctly elevated discal costae, the intervals each with a double row of subquadrate or transverse cells. Anterior coxae contiguous, mesocoxae rather narrowly separated. Tibiae nearly straight, their apices unmodified, each with two small slender and acute spurs. Male abdominal sternite 8 with a deep arcuate median emargination; sternite 8 of female without, or with a very slight, apical sinus.

Key to the Nearctic Species

1. Elytra black or bicolored, each with three discal costae and eight rows of cells ..... **thoracicus** Randall
   Elytra rufous, each with four discal costae and ten rows of cells 2
2. Elytral pubescence comparatively long, evenly distributed; pronotum without median piceous spot; trochanters and scutellum rufous 3
   Elytral pubescence very short, condensed on the costae, the intervals nearly glabrous; pronotum with a median piceous spot; trochanters and scutellum piceous 4
3. Size large, 10-15 mm. in length; ventral surface largely black; mesotrochanters of male spinose ..... **hamatus** Mannerheim

Size small, about 6 mm. in length; ventral surface largely rufous; meso-trochanters of male not spinose ..... **mundus** Say

4. Legs black ..... **aurora** Herbst

Legs rufous ..... **simplicipes** Mannerheim

Dictyopterus hamatus Mannerheim (Pl. I, fig. 2.)

1843. *Dictyopterus hamatus* Mannerheim, Bull. Soc. Nat. Moscou, XVI, p. 245.

Rufous; antennae except basal one or two joints, palpi, tarsi, sides of metathorax beneath, and ventral surface of abdomen except apical segment, black or piceous; scutellum usually dusky basally. Dorsal pubescence comparatively long, not dense, decumbent or nearly prostrate, uniformly distributed, sometimes a little denser on elytral costae. Length 10-15.5 mm.

MALE.—Antennae very slender, nearly two-thirds as long as the body, the median and distal joints parallel-sided and four to five times as long as wide, terminal joint longer; vestiture suberect and bristling except on first three joints. Front with a more or less distinct impression behind antennal prominence; eyes small; clypeus not emarginate. Maxillary palpi rather long and slender, the third joint distinctly longer than wide, terminal joint subtriangular, one-half longer than wide, apex oblique. Scutellum not or very feebly emarginate. Elytra six to seven times as long as pronotum and conjointly at apical fifth three-fourths wider to nearly twice as wide; each with four distinctly elevated discal costae, intervals each with a double row of subquadrate cells, floor of cells smooth and shining. Legs slender; inner apical angle of meso-trochanters spinose, meta-trochanters elongate, half as long as the femora.

FEMALE.—Antennae shorter and less slender, about half as long as the body, median joints two and one-half to three times as long as wide, vestiture not erect; trochanters not spinose, the posterior pair less than half as long as the femora.

ALASKA: Yakatage Beach, VI; Katalla, VII; Ketchikan, VII; Prince of Wales Island, VI. BRITISH COLUMBIA: Terrace; Massett; Graham Id.; Blue River; Skidgate, VI-19; Vancouver; Steelhead, V-28 to VI-21; Pender Harbor, V-13; Trinity Valley, V-20 to VI-4; Cherrieville, VI-1; Creston, IV-30; Fernie, V-28, VII-6; Sanca, IV-24. WASHINGTON: Sol Duc Hot Springs; Hoquiam; Pend Oreille County; Sullivan Lake, VI-3. OREGON: Salem; Santiam N. F., IV-18 to 25; Marion, IV-14; Portland, V-6. IDAHO: Pierce, V-10; Farragut, V-26, VI-3.

Dictyopterus mundus (Say) (Pl. I, fig. 3.)

1835. *Omalisus mundus* Say, Boston Jour. Nat. Hist., I, p. 155.

Rufous; antennae except first two joints, tarsi, and abdominal sternites black, the abdomen rufous at tip in the female. Dorsal pubescence comparatively long, not dense, decumbent or nearly prostrate, evenly distributed. Length 6 mm.

MALE.—Antennae slightly over half as long as the body, median and distal joints about two and one-half times as long as wide, vestiture inclined, not notably bristling. Front not impressed behind antennal prominence; eyes small; clypeus not emarginate. Maxillary palpi slender, terminal joint nearly parallel-sided, one-half longer than wide, apex oblique. Rhombic cell of pronotum not sharply defined, the longitudinal carinae somewhat thickened; scutellum emarginate. Elytra six and one-half times as long as pronotum and conjointly at apical fifth nearly one-half wider, each with four distinctly elevated discal costae, intervals each with a double row of subquadrate cells, floor of cells smooth and feebly shining. Legs slender, trochanters not spinose, the posterior pair elongate, nearly half as long as the femora.

FEMALE.—Eyes smaller; antennae shorter and stouter, scarcely compressed, less than half as long as the body, median joints about one-half longer than wide, the distal more elongate.

PENNSYLVANIA: Lancaster County, VI-1. KENTUCKY: Crailhope, VII-2. NORTH CAROLINA: No definite locality. GEORGIA: (Leconte). LOUISIANA: No definite locality (Horn collection). ILLINOIS: Ware, II-3, in log. ARIZONA: Tucson.

Dictyopterus aurora (Herbst) (Pl. I, fig. 4.)

1784. *Pyrochroa aurora* Herbst, Fuessly's Archiv., v, p. 105.

1835. *Omalisus coccinatus* Say, Boston Jour. Nat. Hist., I, p. 155.

1911. *Eros nigripes* Schaeffer, Jour. N. Y. Ent. Soc., XIX, p. 121.

Black; pronotum and elytra rufous, the former with a black or dusky median spot of variable extent; scutellum black. Dorsal pubescence decumbent or nearly prostrate; longer, finer, and rather sparse on the pronotum; very short, coarser, and rather densely crowded on marginal beads and discal costae of elytra, the interstitial cells nearly glabrous. Length 6.75-11 mm.

MALE.—Antennae slightly over half as long as the body, median and distal joints two to two and one-half times as long as wide; vestiture short, inclined, erect beneath. Front not impressed behind antennal prominence; eyes small; clypeus usually shallowly emarginate; maxillary palpi rather short and compact, distinctly wider to tip, third joint transverse, terminal joint subquadrate, a little longer than wide, the apex feebly oblique. Pronotal carinae well defined; scutellum emarginate. Elytra about six times as long as pronotum and conjointly at apical fifth three-fourths wider, each with four distinctly elevated discal costae, intervals each with a double row of subquadrate cells, floor of cells somewhat opaque. Legs comparatively stout, moderately compressed; trochanters short, not spinose, the posterior pair but little longer than wide and about one-fourth as long as the femora.

FEMALE.—Antennae shorter and stouter, less than half as long as the body, median joints one-third to one-half longer than wide, vestiture not erect.

Distribution.—United States east of the Mississippi River; also known from Minnesota, Arkansas, Arizona, Colorado, Wyoming, Idaho, Oregon, Alaska, British Columbia, Ontario, Quebec, and Newfoundland.

This species is widely distributed over the northern hemisphere, having been recorded from Europe, Siberia, and Algeria. Comparison of American and German representatives failed to disclose any specific differences. Schaeffer described *Eros nigripes* from specimens in which a very fine elevated median line is perceptible within the rhombic cell of the pronotum. This formation is obviously adventitious and without significance.

Dictyopterus simplicipes Mannerheim

1843. *Dictyopterus simplicipes* Mannerheim, Bull. Soc. Nat. Moscou, XVI, p. 245.

1860. *Dictyopterus laetus* Motschulsky, Schrenck Reisen u. For. im Amurlande, p. 115.

Black; pronotum, elytra, femora and tibiae rufous; pronotum with a black or dusky spot usually confined to the central rhombic cell; head often rufous in front; scutellum black. Structure, sculpture, and vestiture exactly as in *aurora,* differing from that species only in the color of the legs. The antennae are extremely unstable, the median joints in the male varying from two to over three times as long as wide. Length 6.5-12.5 mm.

Distribution.—Alaska, British Columbia, Washington, Idaho, Oregon, California, Wyoming (Yellowstone National Park), and Arizona (Hot Springs).

Extreme examples of the males may be selected that would appear to represent two distinct species: *simplicipes,* having the antennae longer and very slender; and *laetus,* with the antennae shorter and comparatively stout. When any large assemblage of specimens from diverse localities has been studied, this diagnosis fails completely, due to the confusing variation in antennal structure. The characters given by Leconte for the separation of *laetus* and *simplicipes,* couplet 3 in his table of *Eros,*[2] are incorrect and of no value.

It is possible that *simplicipes* should be considered a subspecies of *aurora.* In the territory where the two forms overlap there has

[2] Trans. Amer. Ent. Soc., 1881, IX, p. 24.

appeared no evidence of interbreeding, such as would be indicated by individuals with bicolored legs.

Dictyopterus thoracicus (Randall) (Pl. I, fig. 5.)

1838. *Omalisus thoracicus* Randall, Boston Jour. Nat. Hist., II, p. 14.

1838. *Eros praefectus* Newman, Ent. Mag., V, p. 382.

Black; humeri of elytra usually, and rarely sides of pronotum, fulvous; the fulvous humeral spot is usually small but may extend nearly to middle of elytra, it does not attain the lateral margin. Dorsal vestiture decumbent or nearly prostrate, not dense, longer and finer on pronotum, extremely short on elytra except at the humeri, somewhat denser on the costae, otherwise evenly distributed. Length 5.25-8.5 mm.

MALE.—Antennae nearly two-thirds as long as the body, fourth joint longer than two and three combined, median and distal joints about two and one-half times as long as wide; vestiture closely decumbent, not in the least bristling. Front with a more or less distinct impression behind antennal prominence; eyes very large; maxillary palpi slender, rather long, third joint distinctly longer than wide, terminal joint nearly parallel-sided, twice as long as wide, apex feebly oblique. Pronotal carinae very well defined; scutellum emarginate. Elytra six times as long as pronotum and conjointly at apical fifth one-half wider; first, third, and fourth discal costae distinctly elevated, the second lacking; intervals each with a double row of transverse and subquadrate cells, eight rows of cells in all instead of the normal ten; second costa usually feebly indicated at base where there is for a short distance a quadruple row of cells between the first and third costae; first costa more or less obsolete beyond middle, third and fourth costae entire. Trochanters short, not spinose, the posterior pair about one-fourth as long as the femora.

FEMALE.—Eyes small; antennae shorter and comparatively stout, somewhat compressed, nearly half as long as the body, median joints less than twice as long as wide.

MAINE: Millinocket, VI-24. MASSACHUSETTS: Northboro, VII-3; Maynard, VI-18. CONNECTICUT: Litchfield, VI-30; Cornwall, VII-20. NEW YORK: Saranac Inn, VII-9; Buffalo. PENNSYLVANIA: Easton, VII-6 and 18. OHIO: Warren County, Fort Ancient, VII-1 to 9; Delaware County, VII-2. MARYLAND: Suitland, VI-20. TENNESSEE: Fentress County, VI-14. NORTH CAROLINA: Black Mts., VII; Morehead City, IV-23. ALABAMA: De Soto State Park, V-6. FLORIDA: No definite locality. ILLINOIS: Starved Rock, VI-30; Cornland, IV-21; Dug Hill, VII-13. MICHIGAN: Horn Mt. Club; Midland County, North Hadley, VII-15; Cheboygan, VII-13. WISCONSIN: Bayfield. TEXAS: Dallas County, IV-27. CALIFORNIA: 3-Rivers, VI-2. BRITISH COLUMBIA: Terrace. ONTARIO: Sanford, VI, Calandar, VII-19; Ottawa.

EROS Newman

1838. *Eros* Newman, Ent. Mag., v, p. 382.

Similar to *Dictyopterus*, differing essentially in the formation of the pronotal carinae. Starting at the mid-angles of the central cell, the two longitudinal carinae, one on each side, extend convergently forward half way to the apical margin of the pronotum, the cell therefore being open in front. Extending posteriorly from the same mid-angles, the longitudinal carinae converge sharply for a short distance, then continue parallel to each other, one on each side of a deep and narrow posterior extension of the central cell, to the base of the pronotum, the carinae usually converging again and meeting at the base. An oblique carina each side extends from the mid-angle of the central cell to the lateral margin of the pronotum, as in *Dictyopterus*. A strong median longitudinal carina extends from the apical margin of the pronotum half way to the middle, sometimes continuing farther more or less weakly (Pl. I, fig. 1). The labial palpi are similar to the maxillary, gradually wider apically, the terminal joint not abruptly broader than the preceding. The antennae are slender, but distinctly compressed in both sexes. In all other respects the definition of *Dictyopterus* would apply equally well to *Eros*.

Newman did not mention the pronotal carinae in his description of *Eros*, and included thereunder species now assigned to *Dictyopterus*, *Platycis*, and *Plateros*. His designation of *Lycus humeralis* Fabricius as the type of the genus limits it to that species alone in the Nearctic fauna. No congeneric exotic species have been seen.

Eros humeralis (Fabricius) (Pl. I, fig. 6.)

1801. *Lycus humeralis* Fabricius, Syst. Eleuth., II, p. 111.

1835. *Omalisus obliquus* Say, Boston Jour. Nat. Hist., I, p. 156.

1847. *Eros incestus* Leconte, Jour. Acad. Nat. Sci. Phila., (2), I, p. 78.

Black; pronotum with the reflexed sides fulvous, varying to almost entirely fulvous; elytra entirely black or with a more or less extensive humeral fulvous spot, or with basal half to two-thirds fulvous. Dorsal pubescence decumbent or nearly prostrate, very sparse and inconspicuous; longer on pronotum, scutellum, and sutural bead of elytra at base; excessively minute and thinly scattered along elytral costae and interstitial raised lines, the cell floors apparently glabrous. Length 6-9.5 mm.

MALE.—Antennae slender, compressed, half as long as the body, fourth joint shorter than second and third combined, median and distal joints parallel-sided, two and one-half to three times as long as wide; vestiture suberect and bristling except on first three joints. Eyes widely separated, moderately large; maxillary palpi rather long, moderately slender, gradually

wider to tip, third joint not transverse, terminal joint parallel-sided, nearly twice as long as wide, apex somewhat oblique; terminal joint of labial palpi similar, nearly parallel-sided, one-half longer than wide, not compressed except at tip.

Pronotum subrectangular or trapezoidal, one-half to two-thirds wider than long, widest at base; apical margin broadly arcuate, anterior angles rounded but distinct, sides thence subparallel or somewhat divergent to base, feebly re-entrant at basal third or fourth, posterior angles acute, base transverse. Scutellum emarginate. Elytra six times as long as pronotum and conjointly at apical fifth three fourths wider, each with four distinctly elevated and entire discal costae, intervals each with a poorly defined double row of quadrate and irregular cells, floor of cells roughened. Legs rather slender, tibiae straight, trochanters short.

FEMALE.—Eyes smaller; antennae shorter and stouter, feebly compressed, median and distal joints one-half to three-fourths longer than wide, vestiture suberect and bristling as in male.

MAINE: Monmouth, VI-25; Paris, VI-27; Mt. Katahdin, VI-25. NEW HAMPSHIRE: Claremont, VI. MASSACHUSETTS: Berlin, VI-23; Framingham, V-28. NEW YORK: Ithaca, VI-23; Peru, VI-21; Peekskill, VI-14; Lancaster; Buffalo; Hamburg, VI-20; Chautauqua, VI-28; Ramapo, V-28. CONNECTICUT: Cornwall, VI-16. PENNSYLVANIA: Mt. Alto; Columbia Cross Roads, VI-27; Linglestown, VI-24; Dauphin County, VII-3. NEW JERSEY: Ocean City, VII-6. MARYLAND: Odenton, VI-15. VIRGINIA: No definite locality. NORTH CAROLINA: Blue Ridge, McDowell County, V-27; Graybeard Mt., VI-19; Black Mts., VI-20; Great Smoky Nat. Park, VI-14 and 21; Morehead City, IV-23. GEORGIA: Rossville, V-4; Athens. MISSISSIPPI: New Augusta, IV-5. OHIO: Hudson, VII-1. ILLINOIS: No definite locality. MICHIGAN: Oscoda County, W. Br. Big Creek, VI-22; Chippewa County, Whitefish Point, VII-13; Houghton County, Alston, VII-2; Cheboygan County, Douglas Lake, VII-10. IOWA: Lee County, VI-20. ONTARIO: Toronto, V-9, III-19; Prince Edward County, VI-25.

Leconte records the form with basal half to two-thirds of elytra fulvous from MISSOURI, KANSAS, and TEXAS.

PLATYCIS Thomson

1864. *Platycis* Thomson, Skand. Coleop., VI, p. 162.

1879. *Erotides* Waterhouse, Ill. Typ. Spec. Coleop., I, p. 37.

Form elongate, subparallel, slightly wider posteriorly. Antennae simple, rather widely separated at base, slender, over half as long as the body in the male, second joint small. Eyes small; front vertically elevated between antennal sockets in a broad and short truncate process, less prominently in the female, strongly deflexed from crest of process, the mouth inferior but nearly horizontal; mandibles rather slender, arcuate, overlapping; clypeus free; terminal joint of maxillary palpi dilated in the female; labial palpi small, similar in the sexes.

Pronotum subrectangular, the angles well defined; anterior margin broadly arcuate, only slightly advancing and exposing the head more than usual. Pronotal carinae acute and strongly elevated. An oblique carina each side extends from the central cell to the lateral margin just behind the middle. Starting at the inner termini of the oblique carinae, two longitudinal carinae, one on each side separated by about one-third the pronotal width, extend forward subparallel to each other to the anterior margin of the pronotum. Extending posteriorly from the same termini, the longitudinal carinae converge sharply for a short distance, then continue subparallel to each other, terminating well before the base. A very fine median longitudinal carina divides the broad anterior part of the central cell, and may continue more or less distinctly to the basal margin of the pronotum (Pl. I, fig. 1).

Elytra each with four strongly elevated and entire discal costae, intervals each with a more or less evident double row of irregular cells. Anterior coxae contiguous, mesocoxae narrowly separated, trochanters short and unmodified, femora of male each with a pilose fovea beneath near the base.

Platycis is a small and particularly well-defined genus of which five species are recognized in the Junk Catalogue.[3] They range from Europe and the Caucasus across Siberia to Japan and Formosa. The prominent elevation of the front and the foveate femora of the males are unique features not noted elsewhere in the family. Our single species was made the type of *Erotides* by Waterhouse, an apparently unnecessary generic separation based solely on a difference in sculpture of the elytral intervals.

Platycis sculptilis (Say) (Pl. I, fig. 7.)

1835. *Omalisus sculptilis* Say, Boston Jour. Nat. Hist., I, p. 156.

1838. *Eros oblitus* Newman, Ent. Mag., V, p. 382.

1846. *Dictyopterus axillaris* Melsheimer, Proc. Acad. Nat. Sci. Phila., II, p. 302.

Black; pronotum varying from entirely black to entirely fulvous, usually with sides only fulvous. Pronotum virtually glabrous; elytra with minute hairs scattered thinly along costae and margins, pubescence longer and denser on scutellum and sutural bead of elytra basally. Length 5-8 mm.

MALE.—Antennae three-fourths to four-fifths as long as the body (excluding head), outline on inner side subserrate, second joint small, as long as wide, third triangular, similar to fourth and three-fourths as long, median and distal joints two to three times as long as wide; vestiture much inclined,

[3] Junk Col. Cat., pars 128, 1933, p. 39

not in the least bristling. Eyes very small; front trapezoidal before them and horizontal, its anterior margin squarely truncate and acutely raised, its lateral margins somewhat raised in front, merging posteriorly with the feebly elevated antennal prominences, surface alutaceous. Maxillary palpi compact, moderately stout, gradually wider apically, third joint transverse, fourth nearly parallel-sided, twice as long as wide, apex strongly oblique. Terminal joint of labial palpi much wider than preceding joints, broadly triangular, compressed, apex oblique and longer than inner side.

Pronotum subrectangular, one-fourth to nearly one-half wider than long, anterior angles rounded but distinct, lateral margins subparallel to slightly behind middle, thence feebly divergent to the sharply defined posterior angles, base squarely transverse; surface alutaceous, feebly shining. Elytra about six times as long as pronotum and conjointly at apical fifth two-thirds to three-fourths wider; each with four very strongly elevated discal costae; reticulating lines also strongly elevated, forming on each interval a more or less evident double row of irregular cells, the medial dividing line very irregular and frequently interrupted; floor of cells coarsely alutaceous.

Femora stout, each with a shallow elongate-oval fovea on underside extending from base half way to tip, fovea and adjacent surface of trochanter clothed with long hairs; tibiae slightly curved, anterior and middle tibiae minutely mucronate, spurs very small and concealed by the apical setae; abdominal sternite 8 with a deep arcuate median emargination.

FEMALE.—Antennae shorter and stouter, not subserrate, half as long as the body, median joints twice as long as wide; front less strongly elevated. Maxillary palpi dilated, third and fourth joints forming a large clavate mass twice as long as wide, not compressed, outer side curved, apex narrowly rounded, inner side nearly straight, third joint strongly transverse and comprising about one-sixth of the mass. Femora not foveate; tibiae nearly straight, not mucronate, the spurs longer and conspicuous; abdominal sternite 8 without apical emargination.

MAINE: Millinocket, VI-25. MASSACHUSETTS: Berlin, VI-23. CONNECTICUT: Cornwall, VII-5. NEW YORK: Old Forge, VII-6; Allegheny State Park, VII-20; Bear Mt., VII-14; Hamburg, VI-20; Chautauqua, VI-28. PENNSYLVANIA: Castle Rock, VI-30. MARYLAND: Sparrows Point, VII-6. VIRGINIA: Mt. Vernon, VI-20. KENTUCKY: Quicksand, VI-25; Cumberland Falls State Park, VI-25; Crailhope, VI-12; Green County, V-30. TENNESSEE: Gatlinburg, VI-24, VII-5; Smoky Mts., VI-17; Elmwood; Fentress County, Allardt, VI-13. NORTH CAROLINA: Black Mts., VI-12 to VII-14; Graybeard Mt., VI-25; Lake Toxaway, VI-22; Sunburst, VI-7. GEORGIA: Clark County, V-27. MISSISSIPPI: Richton, V-21. FLORIDA: Alachua County, III-16. OHIO: Hocking County, VI-20; Delaware County, VI-21; Monroe County, VII-6. INDIANA: Osborn, VII-4. ILLINOIS: Normal; Edgebrook, VIII-29. MICHIGAN: Paw Paw Lake, VIII-5. MISSOURI: Columbia, VI-9. ONTARIO: Prince Edward County, V-25; Toronto.

LOPHEROS Leconte

1881. *Lopheros* Leconte, Trans. Amer. Ent. Soc., IX, p. 23.

Similar to *Dictyopterus*, differing as follows. Pronotum with an entire median longitudinal carina, and a more or less distinct transverse carina which crosses the longitudinal carina medially and turns obliquely backward at the middle of each side, joining the lateral margin near basal third (Pl. I, fig. 1). The transverse carina may be nearly or quite obliterated. Elytra always with four strongly elevated discal costae. Antennae of male compressed, subserrate, second joint small. Maxillary palpi enlarged or dilated in the female. Mandibles small and quite slender.

Leconte, in establishing the genus *Lopheros* for *fraternus* Randall, failed to recognize the close relationship between that species and *crenatus* Germar, a relationship which is plainly evident when the male genitalia are examined. Both species are apparently rare, *crenatus* in particular having been found in few of the collections studied. An unidentified species of *Lopheros* with dull rufous elytra from Kaolingtze, Manchuria, in the collection of the California Academy of Sciences, indicates a wide distribution for the genus. It is readily distinguished from allied genera by the strongly elevated entire longitudinal carina of the pronotum, usually crossed medially by a transverse carina; and especially by the characteristic structure of the male genitalia.

Key to the Nearctic Species

Pronotum fulvous with a median dusky spot ..... **crenatus** Germar
Pronotum black with a median fulvous spot ..... **fraternus** Randall

Lopheros crenatus (Germar) (Pl. II, fig. 8.)

1824. *Homalisus crenatus* Germar, Ins. Spec. Nov., p. 61.

1838. *Omalisus cruciatus* Randall, Boston Jour. Nat. Hist., II, p. 15.

Form subparallel, very slightly wider posteriorly. Black; pronotum fulvous with the disk more or less dusky medially each side of the longitudinal carina in the two basal cells; varies with pronotum black except reflexed sides and apex. Dorsal pubescence decumbent or nearly prostrate; sparse and comparatively long on pronotum; extremely short and inconspicuous on elytra, confined to marginal beads, costae, and longitudinal intercostae; interstitial cells glabrous. Length 5.25-8.25 mm.

MALE.—Antennae slender, about two-thirds as long as the body, subserrate from joints 3 to 10, second joint small, as wide as long, third broadly triangular, twice as long as second, fourth slightly narrower, triangular, as long as 2 and 3 combined, following joints about twice as long as wide,

diminishing in width distally; vestiture much inclined, not in the least bristling. Eyes small; mandibles arcuate, straight basally, tips not recurving; clypeus not emarginate. Maxillary palpi stout and compact, widening to tip, third joint transverse with inner side very short, terminal joint not compressed, nearly quadrate, apex feebly oblique. Labial palpi small, terminal joint much wider than preceding joints, compressed, broadly triangular, apex oblique and longer than inner side.

Pronotum three-fifths wider than long, widest at base, rounded in front, the anterior angles obliterated, lateral margins slightly re-entrant at basal third, thence diverging to base, posterior angles narrowly rounded, less than right, base transverse; sides, apex, and base rather narrowly and abruptly reflexed, margins somewhat thickened, especially the sides in basal third. Longitudinal carina very strongly elevated in anterior half, transverse carina distinct throughout, rather obtuse. Scutellum emarginate.

Elytra five and one-half times as long as pronotum and conjointly at apical third nearly one-half wider, costal intervals each with a double row of well-defined subquadrate and irregular cells. Abdominal sternite 8 with a deep arcuate median emargination; lateral lobes of aedeagus each with sides and apex broadly testaceous; legs moderately stout and compressed, trochanters short, tibiae nearly straight, unmodified at apex, spurs small and slender.

FEMALE.—Antennae shorter and stouter, scarcely subserrate, median joints about one and one-half times as long as wide. Maxillary palpi dilated, third joint strongly transverse, its apex oblique and forming a broad base for the very large terminal joint, the latter not compressed, its sides widely diverging from the base, outer side nearly twice as long as inner, apex still longer, oblique, apical angles rounded. Abdominal sternite 8 not emarginate.

QUEBEC: Montreal Island; Trois Rivieres, VIII-16. ONTARIO: Rainy River, VII-10. NEW HAMPSHIRE: White Mts. NEW YORK: Gowanda, VI-25; Big Indian Valley, Catskill Mts. MICHIGAN: Marquette, VI-28; Cheboygan, VII-13; Cheboygan County, VII-3; Pentwater, VII-15; Huron County, Sand Point, VI-23. NORTH CAROLINA: Black Mts.

Lopheros fraternus (Randall) (Pl. II, fig. 9.)

1838. *Omalisus fraternus* Randall, Boston Jour. Nat. Hist., II, p. 15.

Black; pronotum with a median subrectangular fulvous spot on basal half or more, varying to almost entirely black; hypomera fulvous with the outer third black. Dorsal vestiture as in *crenatus*. Length 6.5-11.5 mm.

MALE.—Antennae as in *crenatus*; mandibles small and slender, abruptly bent beyond middle, the tips distinctly recurving, scarcely overlapping; clypeus emarginate to accommodate recurved tips of mandibles; palpi nearly as in *crenatus*, less stout. Pronotum three-fourths wider than long, widest at base; anterior angles evident, broadly rounded, lateral margins subparallel to basal third, thence strongly divergent to the narrowly rounded posterior angles, base transverse; apex and base abruptly and narrowly

reflexed, the sides broadly and gradually, margins scarcely thickened. Longitudinal carina of pronotum acutely elevated in anterior half, somewhat obtuse posteriorly; transverse carina partly or entirely obliterated, sometimes indicated by an obtuse swelling of the surface, sometimes in part acutely but feebly elevated. Scutellum emarginate. Elytra as in *crenatus*, the cell floors roughened. Lateral lobes of aedeagus without testaceous borders.

FEMALE.—Maxillary palpi distinctly enlarged but much less so than in *crenatus*. Prosternum compresso-carinate, varying from obtusely prominent, as in the male, to acutely carinate, or (in one example) raised in a triangular lamina nearly as high as long.

MASSACHUSETTS: No definite locality. CONNECTICUT: Cornwall, VII-8. NEW YORK: Buffalo; Boston, VII-10; White Lake, VII-22; New York City. PENNSYLVANIA: Germantown; Montrose, VIII-7; Mt. Pocono, VII-9; Pocono Pines. NEW JERSEY: Oradell, VII-17. OHIO: Scioto County, VI-17. NORTH CAROLINA: Forney Creek, Smoky Mt. Nat. Park, VIII-3; Black Mts., VI-20, VII-3. TENNESSEE: Crabtree, VII-8; Burnt Mt., VII-9.

EROPTERUS new genus

Form elongate, subparallel, very slightly wider posteriorly. Antennae simple, narrowly separated at base, slender, over half as long as the body in the male, second and third joints small and together subequal to fourth. Front short before the eyes, strongly deflexed, mouth inferior, nearly vertical; antennal prominence strongly elevated, completely divided by a longitudinal impression; mandibles small, rather stout, arcuate, overlapping when closed, the tips not recurved; clypeus free, transverse, not emarginate. Palpi similar in the sexes, rather small, the maxillary gradually wider apically, terminal joint not compressed except at tip; terminal joint of labial palpi much wider than preceding joints, compressed, broadly triangular, apex oblique and longer than inner side.

Pronotum subrectangular, widest at base, apex broadly arcuate, anterior angles rounded, lateral margins feebly re-entrant at basal fourth, posterior angles acute, base transverse; sides, apex, and base abruptly and narrowly reflexed, somewhat thickened. Disk with a short longitudinal carina at apex, and an oblique carina each side joining the lateral margin near basal fourth, the oblique carinae sometimes nearly obliterated (Pl. I, fig. 1).

Elytra each with ten rows of subquadrate cells; fourth, third, and usually also the second discal costae distinctly elevated and more or less entire; first discal costa not at all elevated or elevated only at base, sometimes as far as the middle. Anterior coxae contiguous, middle coxae narrowly separated. Legs normal, trochanters short, tibiae unmodified at apex, the spurs small and acute; sternite 8 of male with a broad and shallow arcuate median emargination, lateral lobes of aedeagus sharply acuminate.

TYPE.—*Eropterus trilineatus* Melsheimer.

The principal diagnostic characters of this genus are: the sharply acuminate lateral lobes of the aedeagus; the obsolescence of the first discal costa

of the elytra combined with the distinct elevation of the outer costae; and the three disconnected pronotal carinae—a short longitudinal one at apex and an oblique one each side joining the lateral margin near the base. The third character fails in one species due to the nearly complete elimination of the oblique pronotal carinae.

Key to the Nearctic Species

1. Elytra each tricostate; third antennal joint of male usually distinctly longer than second; sides of pronotum usually pale 2
   Elytra each bicostate; second and third antennal joints of male subequal; body entirely black .....**bilineatus** new species
2. Median lobe of aedeagus extending for nearly half its length beyond lateral lobes, its apical half horizontally expanded 3
   Median lobe of aedeagus extending for much less than half its length beyond lateral lobes, not expanded .....**trilineatus** Melsheimer
3. Median lobe of aedeagus straight in lateral aspect, its dorsal surface with a deep and abrupt channel throughout most of its length; sides and apex of pronotum usually broadly pale .....**rectus** new species
   Median lobe of aedeagus bent slightly downward, without distinct dorsal channel; pronotum usually with the sides and apex narrowly and indefinitely pale .....**arculus** new species

Eropterus trilineatus (Melsheimer) (Pl. II, fig. 10.)

1846. *Dictyopterus trilineatus* Melsheimer, Proc. Acad. Nat. Sci. Phila., II, p. 303.

Black; pronotum with sides more or less broadly and reflexed apical margin fulvous; rarely the apical fulvous border is more extensive. Dorsal pubescence short, much inclined or decumbent, not dense, sparse and somewhat irregular on pronotum, evenly distributed and more plentiful on elytra, sometimes slightly denser on elytral margins and costae; floor of interstitial cells glabrous. Length 4-7 mm.

MALE.—Antennae slender, compressed, subserrate, three-fourths as long as the body, second joint shorter than third, fourth usually longer than two and three combined, median joints two and one-half to three times as long as wide; vestiture erect and bristling except on first three joints. Eyes varying from moderately small to large. Maxillary palpi slender, third joint not transverse, terminal joint three-fourths longer than wide, sides diverging very slightly from base, apex oblique. Pronotum two-thirds wider than long, carinae well defined, median line channeled in posterior half. Scutellum not or very feebly emarginate. Elytra five and one-half times as long as pronotum and conjointly at apical fourth one-third wider; first discal costa not elevated except sometimes at base, other three costae strongly elevated. Front and middle tibiae feebly curving inwardly at tip, metatibiae straight.

FEMALE.—Antennae shorter and stouter, scarcely compressed, not subserrate, fourth joint shorter than two and three combined, median joints one-half longer to twice as long as wide, vestiture inclined; eyes small; abdominal sternite 8 not emarginate; tibiae straight.

Distribution.—United States east of the Mississippi River (no Wisconsin records); also Ontario, Missouri, Arkansas, and Texas.

The variation in the size of the eyes in the males greatly exceeds what would be expected within specific limits, and possibly indicates a confusion of species with similar male genitalia. No decisive characters based on external structure have been discovered for segregating the tricostate species of this genus.

Eropterus rectus new species (Pl. II, fig. 11.)

Black; pronotum fulvous with a roughly quadrate piceous or fuscous spot extending from median half of basal margin two-thirds toward apex, the spot indistinctly defined and sometimes more extensive. Dorsal pubescence similar to *trilineatus*, usually slightly longer, sparser, and less inclined on elytra. Length 5-7 mm.

MALE.—External structure as in *trilineatus*, eyes small, first discal costa of elytra usually quite distinctly elevated in basal half, tibiae not appreciably curving inwardly at tip. Median lobe of aedeagus, as viewed from the side, straight, extending in line with the lateral lobes for nearly half its length beyond them, its distal half horizontally expanded, its dorsal surface with a deep and sharply defined channel from the base three-fourths or more to apex.

Holotype.—Male; Enterprise, Florida, April 18; located in collection of Academy of Natural Sciences of Philadelphia, type no. 8255.

Paratypes.—OHIO: Hocking County, VIII-1. TENNESSEE: Cumberland County, Grassy Cove, VIII-10 to 22; Gatlinburg, VII-15 and 21. NORTH CAROLINA: Southern Pines, V-20; Black Mt., VII-4. SOUTH CAROLINA: Clemson, VII-22. ALABAMA: Mobile. GEORGIA: Fort Benning, VI-7; Stone Mt., VII-6; no definite locality (Horn collection). FLORIDA: Dunedin, IV-11; Enterprise, V-10; no definite locality (Horn and Bolter collections).

The paratypes, twenty males, are located in the collections of Academy of Natural Sciences of Philadelphia (2), California Academy of Sciences (2), Illinois State Natural History Survey (4), University of Michigan (3), North Carolina Department of

Agriculture (1), Ohio State University (1), and the author (7).

Eropterus arculus new species (Pl. II, fig. 12.)

Black; sides and apex of pronotum fulvous, the pale color usually confined to the narrow reflexed edges but sometimes more extensive, or lacking altogether. Dorsal vestiture as in *trilineatus*. Length 4.5-6 mm.

MALE.—External structure as in *trilineatus*, eyes small. Median lobe of aedeagus, as viewed from the side, bent feebly downward, extending at a slight angle with the lateral lobes for nearly half its length beyond them, its distal half horizontally expanded, its dorsal surface without a sharply defined longitudinal channel.

Holotype.—Male: Millinocket, Maine, April 25, 1930, collected by C. Siepmann; located in collection of Academy of Natural Sciences of Philadelphia, type no. 8256.

Paratypes.—CANADA: no definite locality. MAINE: Millinocket, VI-25 and 30; Paris, VII-11. PENNSYLVANIA: Wind Gap, VII-6. WEST VIRGINIA: White Sulphur, VII. TENNESSEE: Crabtree, VII-8; Flat Top Mt., Unaka Sp., VI. NORTH CAROLINA: Cranberry, VI-9; Black Mts., VII.

The paratypes, twelve males, are located in the collections of California Academy of Sciences (5), Cornell University (1), Ohio State University (1), C. A. Frost (1), and the author (4).

Males of the tricostate species of *Eropterus* with the pronotum almost entirely piceous will usually prove, on examination of the genitalia, to be *arculus;* those with the sides of the pronotum broadly pale, and with the apex narrowly so, are usually *trilineatus;* and those having both sides and apex broadly pale are usually *rectus*. Exceptions occur in all three species and only the genitalia provide a certain means of identification. The allocation of females is entirely tentative.

In some examples of *arculus* the median lobe of the aedeagus is apparently grooved, but this is evidently due to wrinkling of a weakly sclerotized surface and is not the same deep and sharply defined channel that occurs in *rectus*. In several doubtful specimens, possibly of *arculus*, the ungrooved median lobe is not in the least deflexed.

Eropterus bilineatus new species (Pl. II, fig. 13.)

Body entirely black. Dorsal vestiture similar to *trilineatus*, rather sparser on pronotum. Length 4-5 mm.

MALE.—Form and structure nearly as in *trilineatus*. Antennae very slender, scarcely subserrate, four-fifths as long as the body, second joint as long as third, fourth distinctly longer than two and three combined, median joints about three times as long as wide; vestiture unusually long, erect and bristling except on first three joints. Eyes small. Palpi similar to *trilineatus*, the terminal joints slightly narrower. Pronotum shining throughout, broad apical and lateral borders with sparse and well-defined circular impressed punctures, the interstices obsoletely alutaceous; apical carina distinct, blunt and very short; oblique carinae nearly obliterated, usually not at all elevated, indicated only by the depressed surface on each side. Third and fourth discal costae of elytra strongly elevated, less distinctly so apically; first and second costae nearly obsolete, more or less evident at base. Tibiae straight.

FEMALE.—Unknown.

Holotype.—Male; Headquarters, Great Smoky Mountain National Park, Tennessee, June 14, 1946, collected by R. R. Driesbach; located in collection of Academy of Natural Sciences of Philadelphia, type no. 8257.

Paratypes.—TENNESSEE: Gatlinburg, VI-26 to VII-21, 1947, collected by R. H. Whittaker, six males in collection of Illinois State Natural History Survey, three in author's collection.

This species approaches closely to *Plateros* in external structure, and could readily be mistaken for a member of that genus. It differs consistently from the other species of *Eropterus* in its totally black color, nearly obsolete pronotal carinae, and bicostate elytra.

PSEUDOPLATEROS new genus

Form and general appearance of *Plateros*, size very small, elongate, parallel. Front short before the eyes, strongly deflexed, mouth vertical. Antennae approximate, short and rather stout, less than half as long as the body in the male, the median joints subquadrate. Maxillary palpi slender, terminal joint parallel-sided, not wider than preceding; terminal joint of labial palpi triangular, compressed. Mandibles small, arcuate and overlapping. Pronotum without carinae. Elytra each with four feebly elevated discal costae, intervals each with a very poorly defined double row of cells. Anterior coxae contiguous, middle coxae rather narrowly separated. Lateral lobes of aedeagus small, suboval; median lobe long and slender, extending far beyond apices of lateral lobes.

TYPE.—*Pseudoplateros moleculus* new species.

In external structure this genus differs from *Plateros* only in the short and stout antennae. The antennal character is incon-

clusive and would not be considered of generic importance without the radically different type of male genitalia accompanying it. The aedeagus of *Plateros* is greatly diversified in structure in the numerous species, but consistently lacks any trace of lateral lobes. In *Pseudoplateros* the lateral lobes are present, although rather small and basal, with the median lobe long and slender and devoid of the distal modifications always found in *Plateros*.

Pseudoplateros moleculus new species (Pl. II, figs. 14 and 15.)

Elongate, parallel, not widening posteriorly, closely resembling *Plateros sanguinicollis* Horn. Black; prothorax and scutellum rufous. The scutellum varies to black, and in one example the body is entirely black. Dorsal vestiture short and sparse, evenly distributed, decumbent. Length 3-3.5 mm.

Male.—Eyes rather small, separated medially above by about one and three-fifths times their length; front with a poorly defined and rather deep subcircular impression behind the strongly elevated antennal prominence, the latter narrowly impressed medially but scarcely divided; antennal sockets subcontiguous; mandibles small, regularly arcuate; clypeus transverse, not emarginate. Antennae compact, short and stout, somewhat compressed, two-fifths as long as the body; vestiture short, not dense, inclined, suberect internally except on first three joints; first joint stout, obconic, one-half longer than wide; second small, slightly longer than wide; third triangular, a little longer than second and one-half wider; fourth as long as two and three combined, nearly quadrate, slightly longer than wide, widest at apex; fifth a little shorter, subquadrate; following joints subequal to fifth, diminishing gradually in width; terminal joint longer, oval. Maxillary palpi slender, second joint elongate, third short, fourth scarcely as wide as second, two-thirds longer than wide, sides subparallel, apex somewhat oblique. Terminal joint of labial palpi rather broadly triangular, compressed.

Pronotum shining, finely punctulate, subpentagonal, one-half wider than long, widest at base, apex broadly rounded, anterior angles evident, lateral margins thence diverging to the subacute posterior angles, base transverse, margins somewhat thickened; sides broadly and moderately reflexed, the base narrowly and abruptly, apex gradually rising; median longitudinal line not carinate in front, channeled in posterior half between subbasal convexities. Scutellum with a shallow arcuate apical notch.

Elytra five times as long as pronotum and one-fifth wider, each with four feebly elevated discal costae, intervals each with a very indistinct double row of cells, the transverse raised lines poorly defined and irregular. Ventral surface shining, sparsely punctulate and pubescent; abdominal sternite 8 with an arcuate apical emargination about two and one-half times as wide as deep, sternite 9 long and slender. Legs rather stout, compressed; tibiae straight, their apices unmodified, the spurs small, slender and acute; trochanters short.

Female.—Unknown.

Holotype.—Male; Pecos, Texas, May 15, 1927, collected by J. O. Martin; located in collection of California Academy of Sciences.

Paratypes.—Texas: Chisos Mts., VII-17-46 (has pronotum black); Davis Mts., VI-9-41; Gillespie County, V-7-46; Uvalde County, V-3-41. The paratypes are located in the collections of Ohio State University (3), and the author (1). All were collected by D. J. and J. N. Knull.

Explanation of Figures

The letters a, b, and c signify, respectively, dorsal, lateral, and ventral aspects.

Plate I

Fig. 1.—Pronota of *Platerodini.*

Fig. 2.—*Dictyopterus hamatus* Mannerheim, male genitalia, Vancouver, British Columbia, IV-1925, K. F. Auden.

Fig. 3.—*Dictyopterus mundus* (Say), male genitalia, Crailhope, Kentucky, VII-2-44, Carl Cook.

Fig. 4.—*Dictyopterus aurora* (Herbst), male genitalia, Mt. McIntyre, New York, VI-11-42, H. Dietrich.

Fig. 5.—*Dictyopterus thoracicus* (Randall), male genitalia, Easton, Pennsylvania, VII-16-30, J. W. Green.

Fig. 6.—*Eros humeralis* (Fabricius), male genitalia, Prince Edward County, Ontario, VI-20-25, Brimley.

Fig. 7.—*Platycis sculptilis* (Say), male genitalia, Crailhope, Kentucky, VI-9-46, Carl Cook.

Plate II

Fig. 8.—*Lopheros crenatus* (Germar), male genitalia, Marquette, Michigan, VI-28.

Fig. 9.—*Lopheros fraternus* (Randall), male genitalia, Mount Pocono, Pennsylvania, VII-9-29, J. W. Green.

Fig. 10.—*Eropterus trilineatus* (Melsheimer), male genitalia, Sparrows Point, Maryland, VII-6-31, J. W. Green.

Fig. 11.—*Eropterus rectus* new species, male genitalia, Enterprise, Florida, IV-18.

Fig. 12.—*Eropterus arculus* new species, male genitalia, Millinocket, Maine, VI-25-31, C. Siepmann.

Fig. 13.—*Eropterus bilineatus* new species, male genitalia, Gatlinburg, Tennessee, VII-20-47, R. H. Whittaker.

Fig. 14.—*Pseudoplateros moleculus* new species, male genitalia, Pecos, Texas, V-15-27, J. O. Martin.

Fig. 15.—Same, antenna of male.

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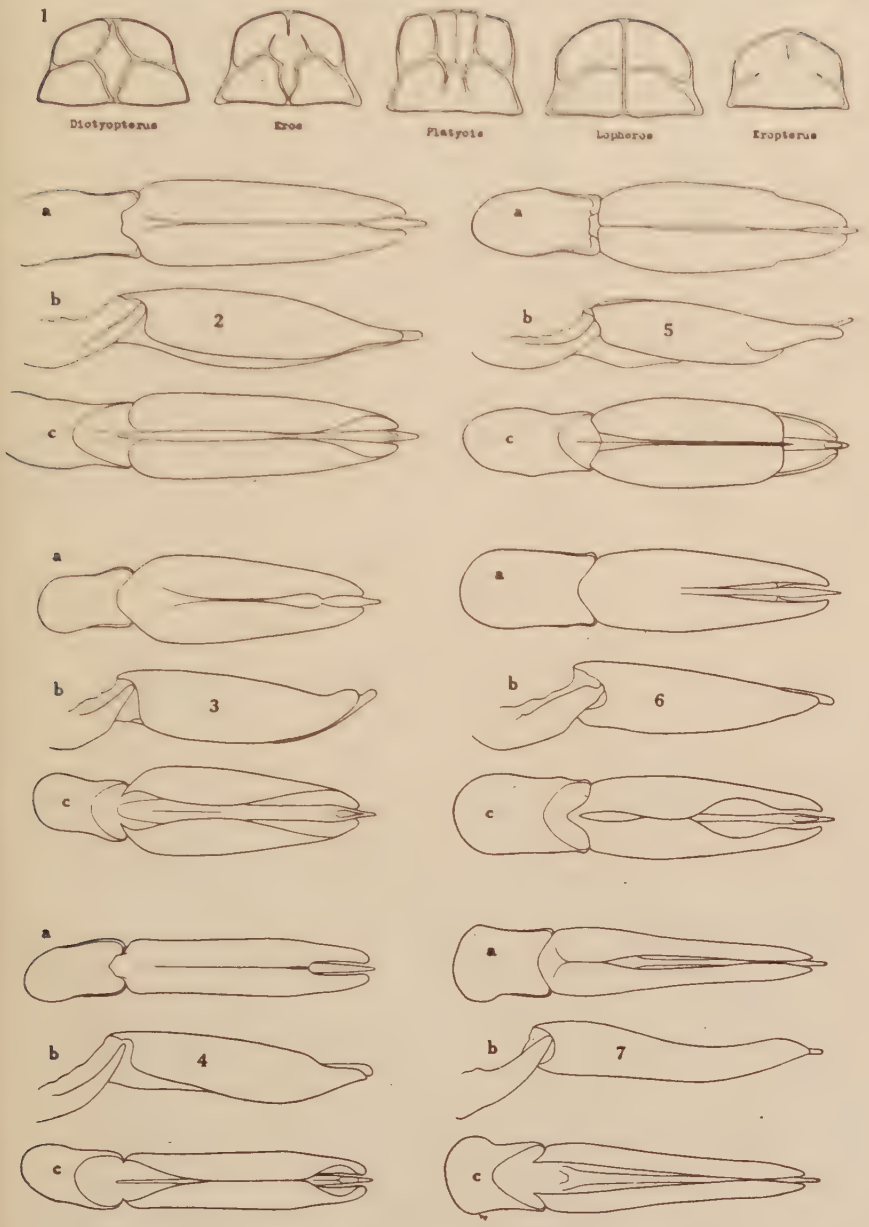
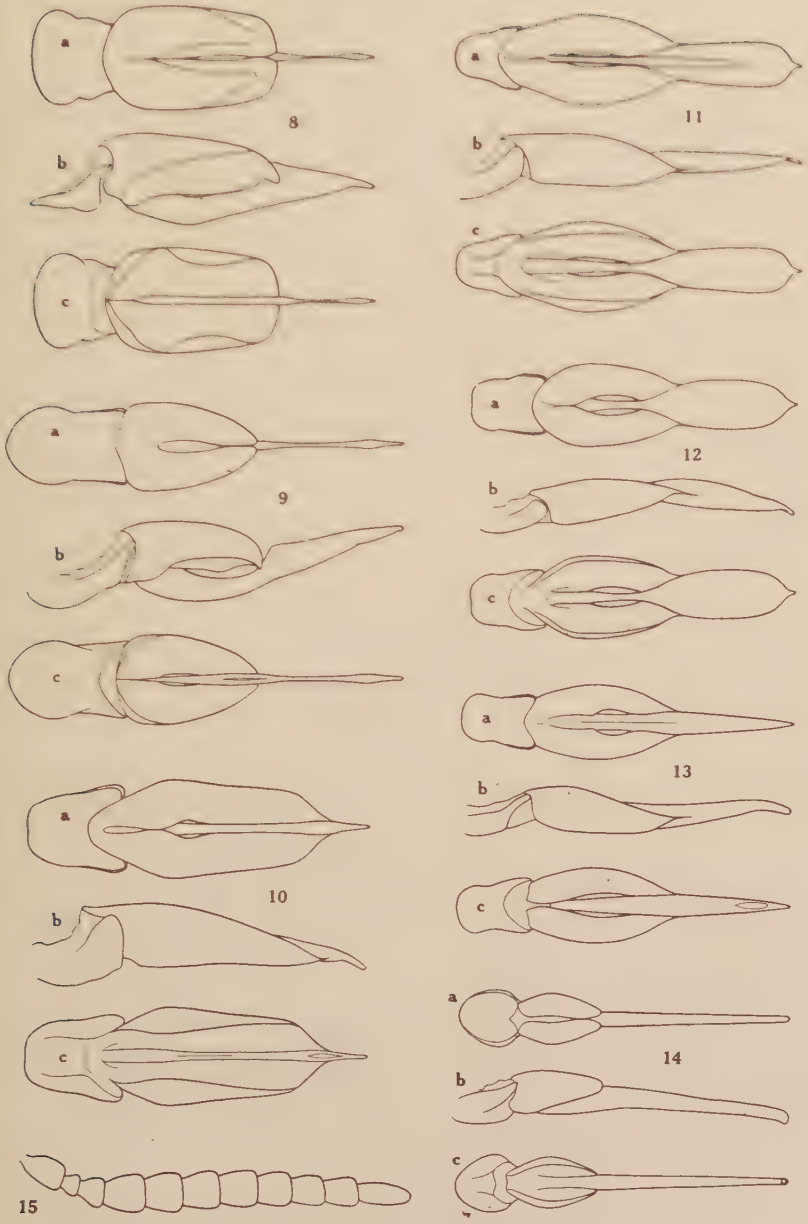


GREEN—LYCIDAE OF UNITED STATES AND CANADA



GREEN—LYCIDAE OF UNITED STATES AND CANADA

PRODROME FOR A MANUAL OF THE DRAGONFLIES OF NORTH AMERICA, WITH EXTENDED COMMENTS ON WING VENATION SYSTEMS

BY JAMES G. NEEDHAM

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(Plates III–V and text-figures)

In the preparation of a new manual of North American dragonflies by Dr. Minter J. Westfall, Jr. and myself, there have come up for consideration a number of matters of interest to entomologists which may not concern the users of that volume, and I wish to put on record here my own opinion concerning some of them.

First, some matters of interest to entomologists generally, and then some that may interest only students of Odonata.

1. *Keys.*—In the making of analytical keys, after correctness in statement of facts, the convenience of the user should have primary consideration; wherefore:

a) The alternative characters to be compared should be placed side by side.

b) When more than one character is stated, the several items in any one rubric should be written in the same order.

c) An Arabic numeral at the right-hand margin, repeated at the left farther on, clearly leads the way to each new rubric of the key and should be plainly marked to catch the eye. As everyone knows, the marking is done in many ways: by indentations of the margin, and by use of numerals and symbols. Over-indentation of the margin wastes space, in long keys much of it. Though the indentation may seem to make the subdivisions of a group more evident, a glance down the right-hand column of names and numerals reveals just the same information.

I think I have tried most of the current ways of key making, and I have come to the conclusion that the simplest of them is

best. I use a dash (–) at the beginning of each alternative member of the rubric, and align the dashes at the left side. It is the function of the dash to indicate a break in continuity and to introduce another idea; therefore it seems most appropriate in this place. Wherefore, for example, a single rubric stands thus:

1—Tarsi 3-jointed; claws toothed 2
—Tarsi 5-jointed; claws smooth 7

2. *Verification Tables.*—The listing of comparable characters in the columns of a table has long been a common practice among systematists, and a useful one. It assembles the characters that are to be compared for more direct comparison, and avoids the lost motion involved in hunting these characters out of their widely separated places in long descriptions. It is a time-saving device of the first order, especially when dealing with large genera. In the new *Manual* verification tables will follow each key to the species, both adults and nymphs, in genera having more than six species.

3. *Figures of Venation.*—Comparison of figures is much facilitated by having the wings all turned in the same direction. Following the precedent set by the principal works on wing venation, all wings will be turned to the right on the page. This follows also the rule, "Show the left side of the specimen," and it is morphologically correct; for the under side is the pleural side of the left wing. It seems fitting also that the reading of the wing characters should go, like that of the text, from left to right. Furthermore, such terms as postnodals (or postcubitals) and post-triangular rows indicate reading in that direction.

Next I will report some changes from the *Handbook* of 1929,[1] and the reasons for them.

4. *Nomenclature.*

a) Four subfamilies (so designated in the *Handbook*) are raised in the *Manual* to family rank: Petaluridae, Cordulegasteridae, Gomphidae, and Aeschnidae, in accordance with modern usage.

[1] *A Handbook of the Dragonflies of North America,* by James G. Needham and Hortense Butler Heywood. Charles C. Thomas, publisher, Springfield, Illinois, 1929.

b) The position of the Cordulegasteridae is shifted to follow the Petaluridae because the adults show in general about equally primitive characters. In placing them formerly near the Libellulidae I was unduly influenced by likeness in form of the nymphs. I now consider that these likenesses are adaptive. They are independent nymphal specializations for similar environment and manner of life.

c) *Erythemis.*—The generic name *Mesothemis* of the *Handbook* is replaced by *Erythemis* in the *Manual.* I was perhaps a little slow about merging the two under the older name; but the species *simplicicollis* (type of *Mesothemis*) is so different in aspect from the other species that I kept it apart until I had obtained nymphs of the type species of *Erythemis, E. peruviana,* for confirmation. When I got that, I found no nymphal characters to justify two generic names.

d) *Gomphus.*—I named as genera several subdivisions of this large genus, and have assigned the species under them (Trans. Amer. Ent. Soc., 73: 307-338, 1948).[2] I will treat these divisions as subgenera in the *Manual,* and call the species all *Gomphus* again, thinking that the average user of this book can get along better without so many names.

e) *Common Names.*—One purpose I had in mind in writing the old *Handbook* was to popularize the study of dragonflies. As a teacher I had learned the futility of trying to get the average educated person to use scientific names. Finding a few common names for species in dragonfly literature, I proposed a few more and brought down on my head a public protest from my good fellow Odonatologist, Edward Bruce Williamson (Ent. News 42: 46-50, 1931). He had found a few persons who, after some tutoring, could talk to him freely in the language of science. He said that anybody could do it, apparently without realizing that hardly anybody *would* do it.

In the *Manual* I have changed some of the common names first proposed and have introduced a few additional. Two examples will show the kind of changes now proposed and the reasons for

[2] This applies also to the group of four small species, the "brevis group," that I have been calling *Hylogomphus,* and that has long been standing in the Cornell University collection under that name.

making them: *Pachydiplax longipennis* I called the Blue Pirate in the *Handbook*. That name did not take; nobody used it. In the *Manual* I am substituting Blue Back, a name suggested by the pruinose blue that covers the back of the abdomen in fully mature specimens. Now quite a number of persons of my acquaintance know this pretty species and always call it by that name. Another is *Coryphaeschna ingens*, that in the *Handbook* I called the Bee Killer. That name was used a little, by some of my bee-keeping friends; but they applied it to several other big darners of bee-eating habits that it would fit just as well. I now propose Sky Pilot instead; a towering name fully justified by the tireless gliding flight of this species, high overhead, through a long season over Southern lanes.

5. *Venation.*

a) The angulation of the midrib of the foot-shaped anal loop in Libelluline dragonflies is one of the most dependable characters for determining relationships among the genera. The degree of bending of the midrib at the angle of the loop is of great significance. I used that character freely in the *Handbook*, but I have abandoned its use in the keys of the *Manual* because many of my students, with no mind for estimating angles even within the wide limits permissible, found it difficult.

b) In the interpretation and nomenclature of the veins I have made no change from the *Handbook*, only a somewhat fuller exposition of it, with a number of added figures, and more emphasis on evolutionary trends within the Order. I have found good characters hitherto overlooked, especially in the cubitoanal part of the wing. They are introduced with adequate illustrations. This system is firmly based on sound morphological principles. It correlates and uses the facts revealed by the study of both comparative anatomy and individual development (ontogeny). It grew out of the life-long studies of Professor John Henry Comstock.

There is another, newer system now clamoring for recognition. It is the latest of several systems successively proposed by Dr. R. J. Tillyard. In succeeding pages I will fully state my reasons for not adopting it. Great confusion has arisen from the shifting of names from one vein to another according to differing ideas as to

where each name belongs. This is a matter of so great inconvenience to all students of insects that I deem it desirable to retell briefly the history and lay bare the basis of the two systems, Comstock's and Tillyard's, and to restate some of the underlying principles involved.

Wing Venation Systems

The Comstock System.—To begin where veins begin, we must go back to the tracheae about which veins are formed. Our first text-figure is a drawing of the tracheae in the wing of a nymph of *Cordulegaster obliquus*. The nymph was a young one about eight millimeters long. The wing sac was one millimeter long.

Text-fig. 1.—Early tracheation in a nymphal wing of *Cordulegaster obliquus* showing the six principal tracheae around which veins later develop. This is a hind wing. The front wing at this stage would be hardly different. (From a camera lucida drawing.)

Springing from a basal tracheal trunk that lies just inside the thorax, there are six tracheae extending out into the wing sac. The names and abbreviations that hereinafter will be used for them are the familiar *Costa* (*C*), *Subcosta* (*Sc*), *Radius* (*R*), *Media* (*M*), *Cubitus* (*Cu*), and *Anal* (*A*).

Our next figure (Pl. III, fig. 1) is from a photograph of a considerably older nymph, the nymph of *Cordulegaster obliquus*. The same six tracheae are shown as seen by transparency within the wing sac. The basal trunk is more highly arched, the tracheae are already very unequally developed. Comparison of this figure and text-fig. 1 shows that the tracheae situated near the middle of the bend in the basal trunk grow out farther and faster, and become more numerously branched. They seem to be better placed in relation to air supply. Succeeding growth will carry

their forks farther out in the wing. Two basal consolidations of veins in pairs are clearly foreshadowed: Radius with Media, and Cubitus with Anal; but no veins have yet been formed.

A later stage in development is shown (Pl. III, figure 2) in the hind wing of *Anax junius*. In this stage the veins are developing about the tracheae. They appear white on a background of gray spongy wing tissue. The tracheae are filled with air and appear black.

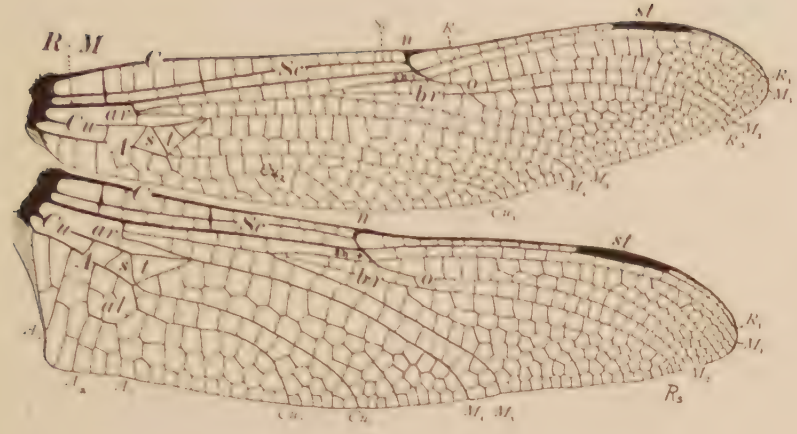
The costal trachea is greatly retarded; the Anal less so, but crowded forward to a contact with the Cubital; Radial and Median tracheae lie close together out to the bend where the arculus will be later; and the radial sector is strongly developed.

A photograph of a well-grown nymph of *Anax junius* is reproduced in Plate IV. It shows the tracheae within the veins, and the nearly complete system of crossveins filling the interspaces between the veins. Beyond the fork of the Cubital trachea its lower branch (Cu2) runs parallel with the terminal branch of the Anal (A1) for a distance and then diverges widely. The four preceding figures show clearly the development of the tracheae through nymphal life.

The wing venation of the adult dragonfly is shown in text-figure 2 and in Plate V. A stout Costal vein occupies the thick front margin of the wing. Radius and Media are fused at the base to look like a single vein. Their union is like that of the two barrels of a gun. Media turns to rearward and meets a crossvein with which it forms the arculus (*ar*). Cubitus runs straight out a little farther than Radius, and then likewise turns sharply to rearward to form the inner side of the triangle—a very important venational landmark. The other sides of the triangle are formed by two long slanting crossveins that converge outward and generally meet at their junction with vein M4.

The Anal vein runs directly outward to meet the hind angle of the triangle (about which, more later). From that meeting point a stout straight vein extends straight backward. It is called the *gaff*. It looks like a simple vein but is not. It is composed of Cu2 and A1, which meet at the triangle, fuse for a short distance, and then separate with strong divergence.

The shape of the nymphal wing changes with growth. At first it is merely a marginal lobe on a fold of skin. When it grows out



Text-fig. 2.—Adult wing of *Cordulegaster sayi*. Long veins: Costa (*C*), Subcosta (*Sc*), Radius (*R*), Media (*M*), Cubitus (*Cu*) and Anal (*A*). Branches are indicated at their tips and numbered from front to rear except for the single branch of Radius, the Radial sector (*Rs*). R + M indicates the fusion of these veins. The parts joining the long veins, named from front to rear, are nodus (*n*), subnodus (*sn*), stigma (*st*), arculus (*ar*), bridge (*br*), oblique vein (*o*), triangle (*t*), subtriangle (*s*), anal loop (*al*).

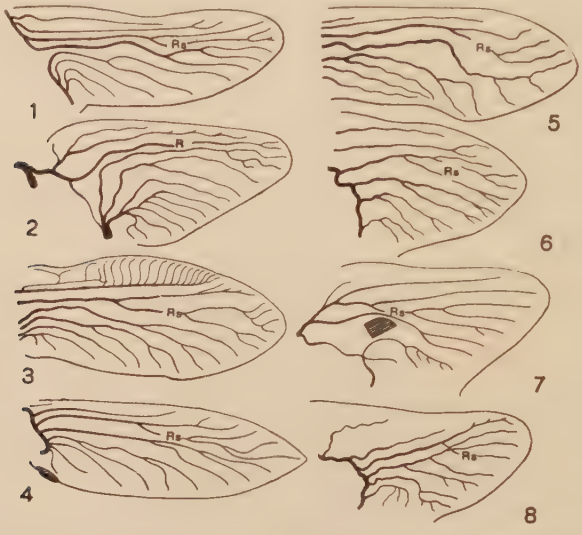
to be about as broad as long, the first terminal branchlets of entering tracheae appear as already shown in text-fig. 1. At the time, and for a considerable time thereafter, the wing is a flattened sac, open at the base, and the tracheae lie free within it side by side. At every molting of the nymphal skin the sac lengthens and the new skin stretches; it also widens, but less rapidly; at the extreme base it widens very little, and through that open base the enlarging wing must be withdrawn at every molt.

As the wing sac grows the middle tracheae steadily increase their holdings. Costa at the front becomes crowded out altogether. The fast-accumulating tissue that will form the thickened and serrulated Costal vein is being supplied by new branches that spring from the front side of the Subcosta and beyond the nodus, from the front side of R1.

At the rear of the wing also the hard-pressed Anal trachea loses some or all of its area to branches developing on the rear side of vein Cu2.

Thus we trace the development of the adult veins from six principal tracheae. The same tracheae are recognizable in the

nymphal wings of generalized members of other orders of insects, as shown in the drawings herewith (text-fig. 3).



Text-fig. 3.—Wing tracheation in generalized members of 8 principal orders of insects: 1. Taeniopteryx (Order Plecoptera). 2. Conocephalus (Order Orthoptera). 3. Sialis (Order Neuroptera). 4. Eriocrania (Order Lepidoptera). 5. Psocus (Corrodentia). 6. Cicada (Hemiptera). 7. Ameletus (Ephemeroptera). 8. Gomphus (Order Odonata).

It is surely not without evolutionary significance that other orders of insects, however diverse their adult venation, have in their wings these same six principal tracheae, in similar relations to a basal tracheal trunk and to each other, with one general type of branching. All have a weak Costa; a longer Subcosta; a strong Radius, bearing on the posterior side far out from the base a distinctive branch, the Radial sector (Rs). All have both Media and Cubitus deeply forked, and all have at least one very variable Anal trachea.

The one considerable difference from other orders is that in Anisopterous dragonflies, trachea Rs lies across the base of the terminal fork of M and extends out to occupy the field between M2 and M3, and stays there. The course it takes in crossing is marked by two apparent crossveins, the Subnodus (*sn*) and the oblique vein (*o*).

Of the six main tracheae the one that gets crowded out altogether is the Costal; the one that gets pushed around most is the Anal. The Anal *vein* stays where first formed in ages past, while under increasing pressure during development the trachea detours.

It is the hypodermis that brings about mechanical improvements, by bending the tracheae progressively out of their easy-going course, and holding the bends by means of strong crossveins.

In the Anisoptera one crossvein holds M and completes the arculus; two crossveins hold Cu, one at each end of its bend, together completing the triangle. One kind of specialization is clearly shown in the preceding figures by the increasing sharpness of the angulation at the bends.

The anal crossing (Ac) takes on the aspect of an ordinary crossvein in the adult wing. The base of the radial sector after it crosses M2, (*o*), also looks like a crossvein. These two crossplaced veins, *Ac* and *o*, though long unnoticed, are among the most constant features of the adult venation. Both are ordinal characters.

The complete dominance of the hypodermis in the final shaping of the venation pattern is seen not only in the sharpening of the bends of big tracheae, but also in the forming *planates* independently of the tracheae across strong tracheal branches. Planates are shown in Pl. III, fig. 2 and Pl. IV, fig. 1, diffuse and shadowy in the younger wings but becoming definite and strong with further development.

All these steps toward the complex venation of the adult wing may be seen in the nymphs of any of our Anisopterous dragonflies if living nymphs of various ages be taken, their wings removed uninjured and given a careful examination with low powers of the microscope.

In the foregoing pages I have sought to show by photographs the nature of the ontogenetic evidence on which the Comstock System is in part based. The photographs speak for themselves.

The Tillyard System.—When Tillyard began the study of dragonfly wing venation, he saw that the pattern of the adult veins is laid down in the wing pads of the nymph by the tracheae that

precede vein formation. For several years he studied tracheation diligently, making large and valuable contributions to our knowledge of it. At first he saw tracheae as an aid to the understanding of the adult venation. Then he carried that idea to extravagant lengths and deemed them all-important. Then he suddenly put them out of consideration altogether as incompetent and irrelevant.

I will let him tell the story of his conversion in his own words, as recorded in successive contributions to the Proceedings of the Linnaean Society of New South Wales, the first phase in three numbers of volume 39, 1914:

Page 180.—" Having now traced the development of the anal trachea through all its stages, we are in a position to give the true homologies " [of the veins].

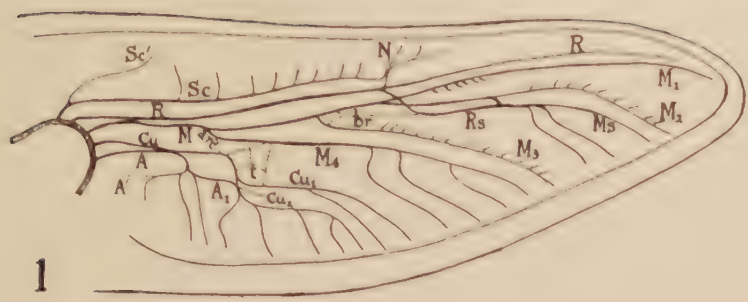
Page 187.—" A satisfactory classification of this subfamily [Gomphinae] has not yet been attained, but a study of the larval wing-tracheation would go far toward establishing it. . . ."

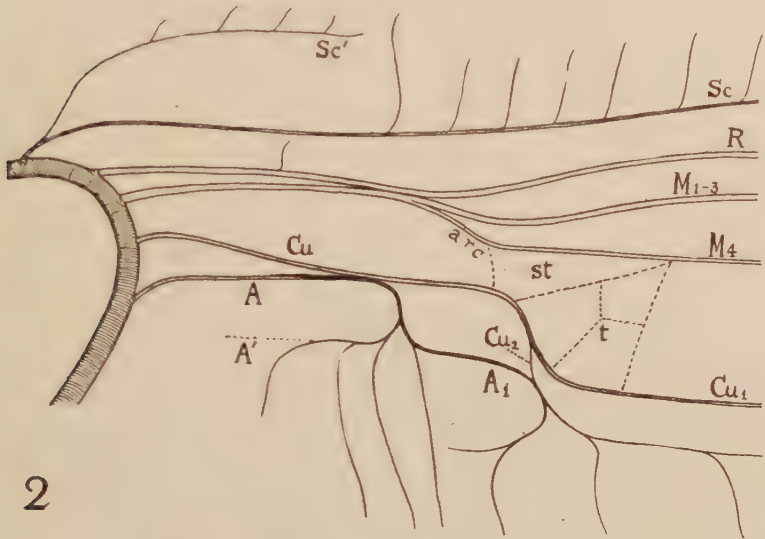
Page 193.—*" Never be sure of the homologies of the parts in any genus of Zygoptera until you have studied the tracheation of the larval wing."* (The italics are Tillyard's.)

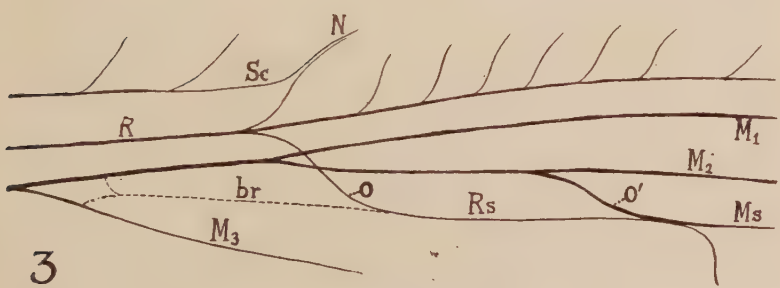
Up to this climax he held that veins must ever follow the paths laid down for them by the tracheae. It was somewhat of a shock for him when he discovered that in adult Zygoptera vein Rs is preceded by a tracheal branch that springs from the median trachea, and that beyond the crossing there is no trachea Rs preceding it. So the radial sector (Rs) of Anisoptera he called the median sector (Ms) in Zygoptera, and published it so in an elaborate table of systems in his otherwise excellent book, " The Biology of Dragonflies " (Cambridge 1917).

Again Tillyard was disturbed by finding that the terminal branch of the Anal trachea (A1), instead of meeting the cubital trachea properly at the hind angle of the triangle as it does in most Aeschnine dragonflies, is replaced in *Hagenius* and other

Text-fig. 4.—Tracheation of nymphal wing of *Uropetala chiltoni*. The lettering by Tillyard is that of the Comstock System excepting Ms and A′: 1. A hind wing entire. 2. An enlargement of the basal part. The label A1 is placed in the area that will be the anal loop. 3. An enlargement of the middle part, showing two oblique veins, *o* and *o′*. (From Entomological News for 1922, Plate I.)







(See bottom of opposite page for legend.)

Gomphines by a branchlet arising from Vein Cu2. This led to the discovery that the base of the anal trachea is out of place, crowded forward against the base of the cubital trachea for a distance, after which detour it goes back to the original level by way of the anal crossing.

In the adult wing this return crossing of the Cu-A interspace (*Ac*) looks like an ordinary crossvein. The vein does not make this detour, but always (when present) develops at the former lower level, well apart from Cu. Again trying to make veins obey tracheae, he named the parts of the adult Anal vein, " Anal bridge or A prime (A′) " out to the Anal crossing; " A " thence to the triangle; and " Cu2b " beyond and rearward to the hind-wing margin. Thus he made a mess of it.

One change of names called for another: ibid. p. 187—

" The ' anal loop ' of *Hagenius,* under these circumstances [tracheal shiftings] is not homologous, in any sense, with the anal loops of the other groups, but is more of the nature of a sub-triangle." [!]

Because I did not concur in this interpretation of the venation, he said (Proc. Linn. Soc. New S. Wales, 40: 224, 1915):

" Needham, however, after noting this fact, is content to allow the notation of the imaginal venation to remain in such a state that the true origin of the so-called anal vein is obscured. . . . I was impressed with the great importance of correct naming for the veins that arise around the tracheae in this part of the wing."

All the above-cited discoveries that were so disturbing to Tillyard had been published and illustrated by me in my " Genealogic Study of Dragonfly Wing Venation," 1903, namely: oblique vein present in *Lestes* but occupied by a branch from the Median trachea; detour of Trachea A, and its return to place by way of the anal crossing (*Ac*) in all Anisoptera; trachea A1 well developed in *Anax* but replaced by a branch from Cu2 in *Gomphus* (l. c. pl. XXXI). He treated all these as discoveries of his own.

Another discovery of great importance was Tillyard's own. It was the presence of two oblique veins in the primitive Anisopteran, *Uropetala.* A branch from trachea Rs is the antecedent of one of them (*o*), a branch from his trachea " Ms," of the other (*o′*). His figures showing these parts are excellent (text-fig. 4) and I copy them herewith (Ent. News, 33: 1, pl. I, 1922). He en-

tirely missed their chief significance. He did not see that in this Antipodean genus he had chanced to come upon a form showing the shift from Rs in progress; that trachea Rs was going out and that his trachea "Ms" was coming in. Thus *Uropetala* bridges the tracheal gap between Anisoptera and Zygoptera.

Tillyard went right on from this point comparing tracheation with venation accurately and consistently in *Aeschna*, *Austrogomphus*, *Hemigomphus*, and in a good series of genera of *Cordulinae* (Proc. Linn. Soc. New S. Wales, vol. 39, 1914), finding only minor, structural divergencies from those cited in the preceding pages. In *Aeschna brevistyla* he found the same shifting of sources of air supply in the last two nymphal instars as are shown in our preceding figures, a branch from trachea Cu2 replacing trachea A1 at next-to-the-last molting. He also found a branchlet that springs from the anterior side of trachea Rs and pushes its way along a zigzag line of bordering hexagonal cells, smoothing it out. This line is not quite straight in the *Aeschna brevistyla* and some other species of *Aeschna*. Persistent little jogs in its course are quite enough to show its secondary nature. When Rs is forked this is its anterior branch.

He showed that in the nymphal wings of Cordulidae there is further reduction of trachea A1. His figures of *Synthemis macrostigma*, half-grown and full-grown nymphs, show that in those half-grown the contact between A1 and Cu2a is loose in the earlier, and close in the later stages. In *Hemicordulia tau* trachea A1 does not reach the triangle at all, Cu2 having fully taken over its area (l. c. p. 179). In *Cordulephya pygmaea*, the same, with the taking-over shared by an enlarged trachea A2. Also a twig springing from M4 has grown down to occupy the outer side of the triangle, a new feature. (*Cordulephyla*, he says, sits like a damselfly with its wings folded together above its back.)

Tillyard's studies of tracheation in the Zygoptera were his greatest single contribution to knowledge of the Odonata (Proc. Linn. Soc. New S. Wales, 39: 163-215, Plate XII). In a single plate he assembled a group of figures that show in parallel columns tracheation and venation of *Neosticta*, *Caliagrion* and *Argiolestes*. These tell remarkably well the story of reduced venation in one Zygopteran line. In *Neosticta vein* Rs has no trachea from any

source, but the merest vestige of *trachea* Rs persists a little beyond the crossing; and then it lies close beside the base of M2, a dim and dwindling remnant nearing the vanishing point. Tillyard offered this very satisfactory explanation of the regressive development that, at that time, he could see going on in *Neosticta* (ibid., 39: 199):

"The trachea Rs must gradually become pressed near its base by the stronger overlying M1 and M2, and if it could not effect a union with the latter by the abortion of its original base, it would inevitably perish for lack of oxygen."

Further evidence of retrogression he found in *Caliagrion* (*ibid.*, 41: 227). His text figure shows still-persisting surface markings that outline the course of trachea "MS" at the old Rs crossing-place.

His parallel figures of the adult venation show progressive disappearance, first of the Anal vein, then of Cu2, and finally of Cu1.

Equally good is his demonstration of the correspondence between phylogeny and ontogeny in Agrionine Zygoptera (Calopterygidae), as shown by the figures on pages 215 and 217 of the Proceedings of the Linnaean Society of New South Wales for 1915.

Up to this point I agree that his evidence of lines of descent is correct and indisputable. If there exists a more complete and satisfactory example of concurrence between ontogeny and phylogeny anywhere in the animal kingdom, it has never come to my attention.

Fine as was Tillyard's presentation of facts by word and picture, his ill-conceived inferences from them were getting him into difficulties. These four were truly bungling:

1. For the posterior branch of the Radial vein he would retain the name Radial sector in Anisoptera, but would call it Median sector in Zygoptera.

2. For the Anal vein he would restrict that name to the part beyond the anal crossing (Ac) and would call the basal part before that crossing "Anal Prime (A′)."

3. Because of the shift of air supply hereinbefore discussed in these pages, he would change the name of the Anal loop (AL) to "Cubito-Anal loop (CuAL)."

4. And to cap the climax, obsessed with the importance of the little oblique vein (*o*), he would establish a Family Lestidae (Proc. Linn. Soc. New S. Wales, 39: 192, 1914 and 40: 228-229, 1915) to contain *Lestes* (*s. lat.*), *Synlestes* and *Epiophlebia*, all of which have the apparent crossvein (*o*), and little else, in common. Strange bedfellows, indeed! *Epiophlebia* is regarded by entomologists generally as being distinct enough to merit a suborder of its own.

He may well have been looking for a way of escape from these entanglements of his own creation. At any rate his conversion came startlingly with the discovery of the wing of a Permian fossil dragonfly, to which he gave the name *Kennedya* (Text-fig. 5). I copy Tillyard's figure of *Kennedya* herewith and quote him again:

"It [*Kennedya*] is very slender, with long petiole [wing stalk], complete nodus and pterostigma, incomplete arculus, and with very few crossveins placed wide apart; e.g., although the wing is very long, there are only four postnodals. This wing solves at once the whole problem of dragonfly venation, and shows what a will-o'-the-wisp we have all been following over the trachea Rs of Needham. The whole vein called M by all odonatologists, inclusive of all its branches and Needham's Rs, is clearly seen to be the true radial sector."

He repeated and extended this statement in his "Insects of Australia and New Zealand," (p. 25) thus:

"A crossing of vein Rs over two branches of Media does not exist. The tracheal crossing is purely a tracheal specialization."

Thus at one bound he went over from an exaggerated evaluation of tracheal control of veins to the opposite extreme.

His only explanation known to me of this change of mind is this one:

"It has been found that palaeontologic evidence is more reliable than tracheation." (Rec. Indian Mus., 30: 153, 1928.)

He gave no explanation of how or why the large body of facts accumulated through many years of careful investigation had suddenly become valueless as evidence of the course of Odonate evolution.

Tillyard went on, after his conversion, putting phylogeny into reverse and involving himself in new contradictions. After basing his system on *Kennedya* he put the Permian fossil *Meganeura* alongside it; *Meganeura,* which has neither arculus nor nodus, but which does have a superabundance of crossveins, and unresolved basal vein connections. Again strange bedfellows! He declared (Afr. Zool., 8: 141):

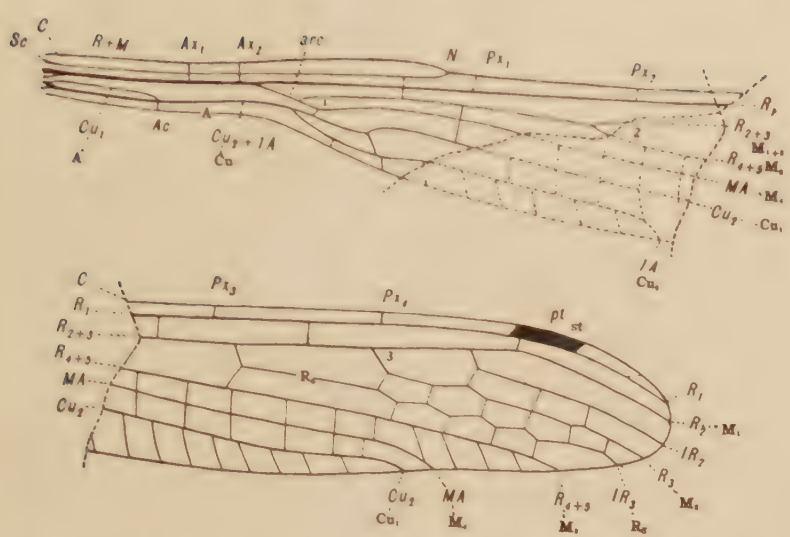
"*Meganeuridae must from now onward be regarded as true Odonata.*" (The italics are Tillyard's.)

Another equally wild phylogenetic flight that entailed a very bad snarl in taxonomy was his decision that *Hemiphlebia* stands

"at the very base of the *Agrioidea* [the Calopterygidae of de Selys] rather than the *Coenagrioidea.*"

He based this judgment on both nymphal and adult characters, but mainly on its lack in the fore wing of the usual crossvein forming the lower part of the arculus, which leaves the midbasal space open internally. Apparently he did not notice that this lack is correlated with a shift in the proximal end of the bridge, which turns to rearward to join vein M3, in such fossils as *Heterophlebia, Tarsophlebia* and others, instead of forward to join M1 + 3, as is more usual.

Kennedya.—Since the Tillyard System is based on the assumption that this little Permian fossil, *Kennedya,* represents primitive conditions for the order Odonata, let us examine it closely. Forgetting for the moment all that we know about trends in specialization of recent Odonata, and neglecting to look backward to see in which direction these trends converge, let us apply a little comparative anatomy to it. Clearly it is Zygopterous and Coenagrionine. It has the same veins that they all have, in the same orderly arrangement only somewhat differently disposed. The Median vein has the usual forks, the first at the arculus, the second beyond the level of the nodus, and the third far out toward the stigma. The second of these forks (marked 2 on the copied figure) is the middle fork (*Mf*). The third (marked 3), is the parting place of veins M1 and M2. In the space between these terminal branches there is a single intercalary sector, as in most of the higher Coenagrionines. The bases of veins M2, Rs and M3 have migrated outward only a little farther than in *Prionocnemis.* The



Text-fig. 5.—The wing of the Permian fossil damselfly, *Kennedya mirabilis* as drawn and labelled by Tillyard for his "Insects of Australia and New Zealand"; a photographic copy. Superadded to Tillyard's lettering is that of the Comstock System in printed letters; added also are the numerals on the three forks of the Median vein and the letter A (for Anal vein) on the hind margin beyond the Anal crossing (Ac).

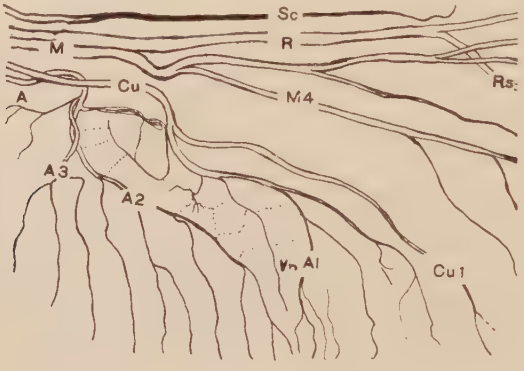
incomplete arculus is swung outward and its arched sectors leave it very much as in *Chorismagrion* and *Hemiphlebia*. The coalescence of the Anal vein with the wing margin is hardly longer than that in *Disparoneura*, and thus the wing is extremely "stalked". Vein Cu1 is arched, much as in *Chorismagrion* and *Synlestes*.[3] The Cubital fork is deeper than in any living species known to me; it extends toward the wing base so far as to form an angle of cleavage between the outer ends of quadrangle and subquadrangle. This is perhaps its greatest departure from the Coenagrionine norm; this and the little loop of the displaced anal trachea that forms a spurious veinlet close alongside the base of the Cubital vein.

For that weak little veinlet which Tillyard so easily identified as the remnant of Vein Cu1, I have a different name. I think it is

[3] To find good venation figures of all these wings in one place, see Dr. Philip A. Munz, Mem. Amer. Ent. Soc., 3: 1-78, 20 plates, 1919.

the Anal vein, shoved under the base of the stronger Cubitus by pressure in hinge formation. It lies in front of and alongside Cu out to the anal crossing (*Ac*), where it descends to its formerly normal level.

Curiously enough, I obtained my first hint of the nature of this veinlet from a crude drawing in a discarded notebook left in my laboratory by a student many years ago. Although it is unfinished, and was not intended by him for publication, for want of a better at this moment I introduce it here, with some lettering that I have



Text-fig. 6.—Drawing of tracheae in the hind wing of a nymph of *Plathemis lydia*, showing the base of the Anal trachea advanced under the base of the Cubital trachea into the midbasal space of the wing. Developing crossveins are indicated only in the area that will become the Anal loop. A vein formed about trachea A in that position would seem to be the equivalent of the vein that Tillyard labeled Cu1 in *Kennedya*. (Portion of a crude drawing from a student's note book; not retouched; merely labeled and trimmed at outer end.)

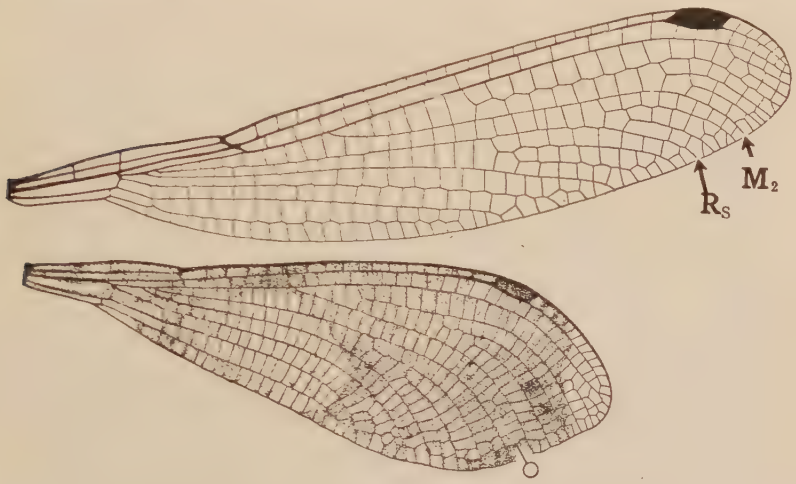
added. It is not uncommon to find the stem of the Anal trachea shoved forward under the Cubital in a nymph of *Libellula*. It is occasionally shoved so far that a clear area appears between the two within the midbasal space. The Anal trachea slips back against the Cubital at transformation to be encased with it as an apparently single vein. The wing base of *Kennedya* is much narrower, and the compression probably greater.

Wherever tracheae develop in a nymphal wing, veins form about them. May it not well be that in the ancestors of *Kennedya* (and *Megatypus* also), this little trachea remained in that far-crossed

position and the vein formed about it there? Veins form about tracheae even when tracheae go farther astray from their normal course.[4]

I can find no reason for assuming that in *Kennedya* the forking place of the Cubital vein was at the extreme base of the wing. Elsewhere in Odonata it is far out at the distal end of the triangle.

The most unlikely thing that I can think of is that Vein Cu1 could disappear and leave no trace. So far as I know the only disappearance of veins from the broad outer area of a wing is that of two short intercalaries from the hind wing of *Pseudolestes mirabilis*. These two are present in the front, absent in the hind, wing. I copy here Lew's drawing (text-fig. 7) showing the space where the loss has occurred. It is the space between veins M2 and Rs. With such a remarkable change in form for so slight a loss of veins, what is the likelihood that a principal vein would go out and leave no trace at all?



Text-fig. 7.—Wings of *Pseudolestes mirabilis*, showing in the hind wing the shrinkage that accompanied the loss of two short intercalary veins between veins M2 and Rs. (Lingnan Science Journal, 10: 230, 1941. Drawing by Dr. Gideon Ting-wei Lew.)

[4] A most aberrant example of this sort (in Ephemeroptera) is figured by Eaton in his Revisional Monograph (Trans. Linn. Soc. London: (2), vol. 3, Zool. Plate VII, 1888).

Even less likely, it seems to me, is Tillyard's parallel and equally gratuitous assumption that half of the Median vein also utterly disappeared. In other insect orders, when principal branches of veins disappear, they generally leave some signs of the manner of their going—often intermediate stages and concomitant readjustments.

Is it not more rational to say that Median and Cubital veins have here the usual forkings: Media four-branched and Cubitus two-branched? It certainly aligns the Odonata better with other orders of insects and imposes less strain on the imagination. Why create IR3 and suppress M1 and M2? I cannot see how any modern dragonfly can have had such a stalk-winged, few-veined form in the line of its ancestry. Far from being primitive, it stands at the peak of its own peculiar line of Zygopterous specialization.

I think that *Kennedya* was an isolated freak in Odonata evolution that developed early and lost out entirely in the struggle for existence.

The guess that *Kennedya* is primitive contradicts zoological experience generally; for elsewhere in the animal world the primitive forms have much duplication of parts; parts that in the more specialized forms are reduced in number and differentiated in form and function.

And in other insect orders, genera that have many-veined wings are now placed near the foot of the series. For example, near the foot in Diptera are the crane flies, of the family Tanyderidae; in Hymenoptera, the sawflies (Tenthredinidae); in Lepidoptera, micro-moths of the Micropterygidae; in Neuroptera, *s. lat.*, the Corydalidae; in Ephemeroptera, the Ephorons (Campsuridae); in Plecoptera, the larger stoneflies (Pteronarcidae); and in the Trichoptera, *Rhyacophila.*

This judgment as to their lowly status is not based on their many-veined wings alone, but also on other supernumerary parts, and on their general crudeness and their greater likeness to the more generalized members of other orders—convergence backward toward a common ancestry in evolution.

When Tillyard found the wing of *Kennedya mirabilis* and announced to the world that it "at once solved the whole problem of dragonfly venation," he then bid us all follow his lead by a state-

ment that reads like an imperial edict (Ent. News, 34: 396, 1934):

"I wish here . . . to close up, once for all, the erroneous lines of thought, which I, in company with almost every other student of Odonata, had been following for many years."

He spoke like an oracle. He was obeyed like one by a few good entomologists. Even Dr. Ris, great Odonatologist though he was, seemed baffled for a time by Tillyard's clamor (Proc. Linn. Soc. New S. Wales, 39: 165, 1914). He never adopted Tillyard's System; nor did Calvert; nor did Williamson.

The Radial Sector.—Several other entomologists balked at the idea of the crossing of the radial sector. The reason that they gave for their dissent was often expressed in three words: "Veins cannot cross."

Quite true; veins cannot cross—they are a fixed part of the exoskeleton—but tracheae can. They could and did cross in the beginning of the dragonfly line of evolution or they would not be crossing in all anisopterous dragonfly nymphs today. Like all other parts of an animal they follow the beaten ancestral path in their postembryonic development, in absence of obstacles great enough to turn them aside.

This crossing of trachea Rs must have occurred very early in wing evolution while the wing was a roomy open sac—a mere baggy fold of skin. It still occurs while the wing is in that early condition. It can hardly be thought of as occurring after the flattening and the internal fusion of the two layers. Trachea Rs crosses as soon as formed and stays crossed while adult vein Rs develops about it.

I do not know why trachea Rs crosses M1 and M2; I do not know why the optic nerves cross under every vertebrate brain; but the fact of these crossings is undeniable.

In my first report on tracheation in Odonata (Amer. Nat., 32: 903, 1898) I made a mistake in regard to the time and manner of the crossing by trachea Rs. In figure 60B I showed Rs ending between M1 and M2. Since then I have examined dozens of nymphal wings of about that same age and I now feel sure that what I then represented as a second crossing of M2 by Rs was merely a meeting of the two by converging bends and then a separation. They touched but did not cross. I have seen that contact

several times. A light pressure on the cover-glass of a specimen freshly mounted in water will spread them apart. I have acknowledged this error before (Jour. N. Y. Ent. Soc., 43: 113-129, 1935), but I mention it again because, inconsequential as it was to phylogeny, Tillyard made it appear as invalidating all evidence from tracheation. So far as ontogenetic evidence is involved, the situation is improved by that truer exposition of the facts; it leaves no second crossing to be explained.

It was a great puzzle to me when I first found that in the nymphs of Zygopterous dragonflies trachea Rs is almost wanting, and that a branchlet from trachea M2 has supplanted it. The explanation now appears simple. The wing cases of the Zygopterous nymphs are much thinner from the beginning of their development. There is less room in them for a tracheal crossing. The squeeze at the base of fork M1 and M2 seems to have blocked the entrance of the air into the field of the Radial Sector.

The tissues must have oxygen in order to live. When one source of supply is waning, another must be found. What is more to be expected than that new sources of supply should be found? The oxygen demand of the tissues in the area supplied by Rs appears to have been met by the ingrowth of tracheal branchlets from the nearest available bordering sources, tracheae M2 and M3. These branchlets arose at different levels: far out in *Lestes;* well toward the wing base in most Agrionidae.

In a few Zygoptera the oblique vein (*o*) persists as a sign of the former crossing. It stands in a row of perpendicular crossveins aslant in the direction that trachea Rs gave it when first formed. In most Zygoptera it is lost, and in some it may or may not be present as individuals vary. The base of trachea Rs, around which was formed the subnodus (*sn*), persists in all Odonata, that portion of it having become a permanent part of the strong framework of the wing.

We must take account of what goes on in the trachea at the time of the last renewal of the nymphal skin in order to understand how such a shifting of air supply is possible. Tracheae, as every entomologist knows, are formed by ingrowth of the skin of the body from its surface at the spiracles. They are tubular in form. They attain great length. By their branching and rebranching

they make contact with all the living tissues of the body and bring them oxygen. Their walls are composed of a single layer of hypodermal cells. The cuticular linings of the tracheal tubes have developed hard rings of chitin (*tracheids*) on the inside. These tracheids serve, like the metal rings inside a steam hose, to prevent the collapse of the tube. They keep the tracheae open for the passage of air.

When the cuticular linings are withdrawn at molting, they carry with them all their content of air. The bare hypodermal walls of the tube remain in the body, and are soft and collapsible. A new supply of air enters at the spiracle. It pushes along gradually refilling the tubes and all their branches, while tracheids and new tracheoles are being developed. Blocked in its original course by compression, the air, following lines of least resistance, enters the field of Rs from neighboring tracheae.

In the suborder Zygoptera trachea Rs is not found beyond its crossing in the very much thinner wings of that suborder. The air supply from Rs becoming inadequate, new tracheal branchlets from the bordering veins gradually encroached upon that field to meet the oxygen demand of the tissues there. Part of the field seems to have been saved in that way; part of it seems to have been lost; for the interspace between veins M2 and M3 is reduced in Zygoptera.

One feature in the venation of Anisoptera that seems to have had its source far back in the evolution of the group is the undulation of veins M3 and M4, opposite the oblique vein, the place where vein Rs turns toward the wing border. This sag occurs in the more primitive families, and in the more primitive genera of all families of Anisoptera. It suggests that these two branches of Median M3 and M4 were once elbowed a little out of course by the crossing of trachea Rs over into their territory.

This sag of veins M3 and M4 still lingers in at least one of the more generalized members of the suborder Anisozygoptera, as shown by Tillyard's figure of *Gomphites brodiei* (British Museum Fossil Insects, 1: 34, 1925). Since it disappears with specialization in all the larger modern families, it may be considered as "on the way out"—a crumbling landmark, so to speak.

Quite different is the undulation seen in veins M2 and Rs in the wings of *Libellula* and its near allies (Group III of Ris's "Libellulinae") for that can be traced upward through the genera of the group. It seems to be coming in, for there is a parallel development of it in isolated genera of other groups or tribes; for example, in *Dythemis,* in *Tholymis,* and in *Pantala.*

Wing Fluting.—Tillyard was edging over into the field of paleontology when he came upon Lameere's theory [5] of the evolution of insects. He found it much to his liking and he adopted it at once, and based his new system on it.

Lameere held that the fundamental plan of insect wings in general is one of regularly alternating high and low veins, high and low occurring in pairs, each high vein having a companion low vein or a low posterior branch; the whole wing having in consequence a fluted surface. High Costa had its low Subcosta; Radius, its sector; Media, its two divisions, front high, rear low; Cubitus, the same; and so on from front to rear with alternating simple Anals sometimes present.

Lameere's theory was beautiful in its simplicity and so easy to apply that some entomologists seemed to think it must have been Mother Nature's own idea when giving wings to insects. However, it was not entirely original with Lameere. It is in substance very like the theory that Adolph [6] presented 43 years earlier, for general rejection.

Lameere's theory, like Adolph's, was based on the venation of adult wings, and took no account of tracheation. He charged that Comstock's "primitive type" did not show the full complement of veins possessed by primitive insects; and that Comstock did not take sufficient notice of the longitudinal fluting of their wings caused by alternating high and low veins. Lameere found more veins and more regular fluting of the surface in mayflies (Ephemeroptera), and in certain many-veined fossil Palaeodictyoptera, and he based his theory mainly on what he saw in these.

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[5] Lameere, A., "Sur la nervation alaire des insectes." (Bull. Acad. Roy. Belg., pp. 138-149, 1922.) A translation by Austin M. Brues was published in Psyche, 30: 123-132, 1923.

[6] Adolph, G. Ernst, "Ueber Insectenfluegel." (Nova Acta, K. Leopold-Carol. Deutschen Akad. Naturf., 41: 215-291, 1879.)

He did not seem aware that Comstock had once adopted Adolph's System, and tried for some years to match the veins of the wings with the high-and-low plan.

In designating individual veins Comstock, like Redtenbacher, first used Roman numerals, odd numbers for high, and even numbers for low, in regular succession. He used these labels in the first edition of his "Manual for the Study of Insects," omitting two low veins, Redtenbacher's V and VII, toward the middle of the wing; veins that the theory called for, and that he could find no veins to match. He used that system in his essay, "Evolution and Taxonomy," that was published in the Wilder Quarter-Century book in 1893 (Ithaca, Comstock Publishing Co., pp. 37-114). On page 68 of that work, his table of succession of high and low veins is quite like Tillyard's latest table, showing the same sequence save in its use of Roman numerals instead of capital letters for vein labeling. (Comstock's *Manual* was my first text-book of entomology, and from it I learned to designate the veins by these Roman numerals.)

Comstock gives a brief statement of his experience with the Adolphian System on pages 4 and 5 of his book, "The Wings of Insects." After years of trial he found the Adolphian theory wholly artificial and misleading and abandoned it.

Lameere, in introducing his theory, was quite mistaken when he said in substance that Comstock's "typical insect wing" was derived from tracheation and based on the venation of the Plecoptera. I know that it was based on comparative study of adult wings in all orders both recent and fossil, but mainly Lepidoptera and Diptera, and was established in his mind and published in his writings long before his studies on wing tracheation were begun.

Lemche similarly misconstrued Comstock's Typical Insect Wing in his paper on the Origin of Insect Wings (Vidensk. Medd. Dansk. Naturh. Foren., 104: 127-168, 1940) when he said:

"Comstock's '*Primitive Type*' will not stand scrutiny. The original number of veins must have been somewhat large and quite indefinite."

Comstock's typical wing represents rather the survivors of the struggle for existence among the larger number of competing veins,

at a point far enough back in vein evolution to serve as a standard of comparison for all the winged orders; and that was all that he claimed for it. Comstock wrote (Amer. Nat., 32: 83, 1898):

"It should be borne in mind that our main object at this time is merely to trace the homologies of the wing-veins, to the end that a uniform nomenclature for all orders can be adopted, and also to enable us to make intelligent use in taxonomic work of the characters presented by them. We do not presume to say that we have definitely determined the peculiarities of the venation of the wings of the stem form from which winged insects have descended. We feel, however, that we have reached a sufficiently near approximation to this desired end to warrant our conclusions regarding the homologies of the wing-veins, and to enable us to commend a nomenclature for them which we believe can be accepted as final."

Probably a larger number of tracheae entered the wing-pads of the earliest nymphs. The six herein discussed are those that fell into a workable mutual adjustment and drew down the basic venation pattern.

Fluting is one way in which wings are stiffened: a primitive way; a poor way, apparently, for it is fully carried out in *Ephemeroptera* only, and in that order is most complete and regular in the most highly specialized *Baetine mayflies*.[7] Mayflies are all weak flyers.

A simpler plan of support for the outer half of the wing prevailed among the higher insects and yielded the best flyers. A simple joining together of long veins, the *cord*, is a chief element of their framework. The cord may have been first formed by the strengthening of those crossveins that stood at the points where forks came nearest together; that hitched them together at the elbows, so to speak.[8]

Tillyard was among those most eager to apply Lameere's theory, and especially eager to apply it to Odonata, that order being considered most nearly related to Ephemeroptera, and the Ephe-

[7] This matter is discussed and illustrated in the book, "The Biology of Mayflies," by Needham, Traver and Hsu. Ithaca, New York, 1935, pp. 115-131.

[8] This matter I have discussed more at length in a brief study I once made of the crane-fly (Tipulid) wing venation (Bull. N. Y. State Mus., 86: 220-224, 1907).

meroptera being a principal source of the inspiration that brought the theory to its rebirth. So he began a diligent search for pairs of high and low veins. And very soon he was proceeding with a dash that far surpassed all his past performances. In 1925 he offered a complete new system (Amer. Jour. Sci., (5) 10: 7) of vein labeling. He used the same names and abbreviations for veins as in the Comstock System, but after the first two pairs, C-Sc and R1-M1, he applied the names to different veins than in that system. His third pair, M1-M1a, initiates a discord that continues all the way to rearward. Only by omitting Rs altogether and creating in its stead a new independent vein, and by assuming that M3 and M4 had completely fused, could Tillyard make the venation conform to Lameere's theory. Thereafter anything that stood in the way of the high-and-low vein succession was banished, either as a "tracheal specialization" or a result of "mechanical necessity," without a word of explanation as to how the tracheae comport themselves or what purpose the mechanics serve.

In 1926 he offered a second "new notation" (ibid., (5) 11: 130; also in his "Insects of Australia and New Zealand," p. 68) with all the vein labels moved again, to positions where he thought they better fitted Lameere's theory, judged by convexities and concavities of veins (of which he could never be quite sure).

Tillyard's earlier replacement of Rs with Ms had caused little or no inconvenience; but this later translocation of names by two new systems wrought chaos. Now that both have been used by a few Odonatologists in works of considerable importance, the confusion they initiated is handed on to future generations.

Tillyard's difficulty was just the difficulty that any one will have if he seriously undertakes to find in the middle of the dragonfly wing alternating pairs of high and low veins to fit Lameere's theory, simply because they are not there.

I search the dragonfly wing lying before me for ups and downs and this is what I see: at the base in Anisoptera, Zygoptera and Anisozygoptera alike, the entire framework of the wing stands on a consolidation of five vein stocks: Costa high; Subcosta low; Radius plus Media very high; Cubitus low; Anal high.

At the front border before the nodus I see Costa and Radius, both high veins, with Subcosta, low, lying between them in a deep

groove, braced against both high ones and solidly fused with both at base and tip. Beyond the nodus Subcosta disappears, and the Costa becomes a low vein. (More of this later.) Veins M1 and M2 are about equally low, in consequence of which the area between them is a more or less flat-bottomed trough rather than a low-vein groove. Vein Rs is high and strong; running on the summit of a ridge. Vein M3 is low, M4, high; similarly, Cu1, low and Cu, high. (These are parallel pairs.) Farther to rearward there is no semblance of Adolphian alternating ups and downs.

What one sees on looking edgewise at a wing is not so much fluting from base to tip as little counterbalanced slants, overarchings and bellyings in definite areas. As a whole the wing is less broadly concave underneath than a bird's wing, but has little areas which, in action, fill with air on the down stroke, and probably hold against the down-pull of gravity.

Of more fundamental importance than longitudinal fluting of the wing surface is the grouping of the veins at the base of the wing into two sets: a Costo-Radial group at the front and a Cubito-Anal group at the rear. These go back in origin to the two corresponding groups of tracheae that in the beginning entered the wing pad from front and rear.[9] They are still quite separate in stonefly (Plecoptera) nymphs.

Most of the other orders of insects have developed better cross-bracing by bending and fusions of veins, by reduction in numbers and improvement in strength and placement of crossveins.

There is a measure of fluting preserved in all the winged orders. There is still some fluting in wings of the Odonata. Indeed there is more of it than the Neo-Adolphians have ever noted in print. There is obliquely-transverse fluting in the field of the two planates, *Rpl* and *Mpl*. Crossing each of these planates is a series of low veinlets that develop about the rearward-running branchlets of tracheae Rs and M4. They are well shown in our Plate V.

Tillyard's Corollaries.—With Tillyard fixed upon *Kennedya* as the most primitive known member of the order Odonata, and Lameere's version of the Adolphian fluting theory taken as his guide, let us see how he gets on.

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[9] See Chapman's chapter in Comstock's *The Wings of Insects*, 1918, pp. 27-51.

First he assumes that veins develop before tracheae, which is so patent an error, so contrary to what any one may see who will take the trouble to look at the development of nymphal wings, that it merits no further notice.[10]

Next he assumes that the veins start at the wing margin and grow inward (Amer. Jour. Sci. 9: 332, 1925)[11] toward the base, and that the tracheae later "find their way into them;" but he does not explain how the tracheae find such a devious way into the veins, and with such constancy of form; nor does he explain how adding substance at the wing margin affects flight.[12]

[10] I should not omit to say, however, to any one who wants to see the facts with his own eyes, that Tillyard once gave excellent directions for preparing nymphal wings for the microscope. (Proc. Linn. Soc. New S. Wales, 39: 204, 1914.)

[11] This idea of inward growth was not original with Tillyard, or at least it is quite the same thought that Woodworth put forward in 1906. (Woodworth, C. W., "The Wing Veins of Insects." Univ. of Calif. Techn. Bull. Entomology, 1: 1: 1-152, 1906. See also my review of this article in Science, xxv: 218-223, 1907).

[12] A very simple experiment that any one may repeat on a fair day when living dragonflies are available, will show this. It was first performed by Dr. Frank Lutz and myself to settle a discussion of the mechanics of insect wings. We went to the Cornell University Fish-Hatchery ponds, where *Libellula pulchella* was flying in such numbers that we thought a few specimens might be spared for scientific use, and we caught them one by one for a few trials of their flight efficiency under varied wing areas:

No. 1, with both fore wings clipped off, flew swiftly and steadily away, on hind wings alone, and disappeared in the distance.

No. 2, with both hind wings removed, likewise flew away, on fore wings alone, only a little less steadily.

Nos. 3 and 4, with only one wing removed, fore or hind, respectively, flew away much less steadily, but kept going.

No. 5, with the weight of the body of another specimen suspended by a silken thread approximately under its center of gravity, flew away swiftly as if unimpeded by its load. (We had taken no scales for weighing the load.)

No. 6. With this one we came to the point of our field quest: the effect of adding weight at the outer margin of the wing. For the purpose I had brought a small tube of liquid glue with which I laid a fine line of the glue along the hind margin of all four wings. (There is no contact between the fore and hind wings. The glue adds very little weight.) The specimen thus treated, when liberated flopped slowly to the ground at a distance of a few meters.

No. 7. The same specimen, recovered and trimmed of every bit of glue-covered wing membrane and again liberated, flew swiftly away and disappeared in the distance. One may ask:

"How then could flight have been maintained through the developmental years or ages if the veins were lacking a basal connection for support?"

The effectiveness of the insect wing is dependent on thinness and pliancy at its hind margin. Those Neuroptera that have preserved an outer marginal vein have never attained to any special proficiency in flight.

Finally, in order to complete his renunciation of the "erroneous lines of thought" that he had once professed, Tillyard banishes hexagons from the network of Odonate wings (Austral. Zool. 9: 135, 1933).

"The Odonatoid and Plectopteroid [Ephemeroid] orders differ from the Palaeodictyoptera in not possessing a primitive archedictyon of weakly chitinized cells. Instead, their crossvein system is chiefly made up of single crossveins, strongly chitinized and placed more or less at right angles to the veins that they connect. Only in special areas of the wing, where a larger space than usual is left between branches of main veins, are polygonal cells developed. . . . An abundance of crossveins is to be regarded as a specialization by addition". (Austral. Zool., 9: 135.)

To accept this idea one must disbelieve what he sees, and also what he knows about the nature of the wing substance.

Assuredly the entire wall of the nymphal wing sac from first to last consists of a single layer of hypodermal cells, which secrete a transparent cuticle on their outer surface, and renew the cuticle at every molt. Clear membrane between the veins appears only with the last molt at time of transformation when the final great stretching occurs. The two layers of the sac are then fused, and the old cuticle is loosened and ready to be shed. All is soft underneath it. The changes to adult form are already well begun. Abundant material (molting fluid) for the new cuticle is accumulated under the old. All is turgid. Then blood pressure from within ruptures the old skin and gives release.

The final shaping of the wings is mainly a stretching process made possible by the viscosity of the semiliquid substances of the hypodermal cells and the quick-hardening capacity of the outer layer that will form the new cuticle on exposure to the air.

Veins are formed by massing of hypodermal cells about tracheae. Crossveins are formed out of the tissue cells left in the interspaces, their size and position being determined by the viscosity of that tissue; by how far the less-fluid pigment-bearing substance beneath the cuticle will stretch and leave the membrane clear.

It seems probable that the stretching in the beginning yielded an irregular network of veinlets—*archaedictyon* (ancient network) Tillyard aptly called it—over the whole surface of the interspaces

between the veins. Such a network is characteristic of many of the fossil Palaeodictyoptera. Archaedictyon persists in the feeble wings of termites; in the wider interspaces of the clumsily flying big stoneflies (*Pteronarcys*, *Dictyopteryx*); at the unexpanded extreme base of the fore wings of some Orthoptera; and elsewhere. Reduced to a more orderly pattern of hexagons, it still fills the outer, wider interspaces of the more generalized Anisopterous dragonflies. In a truly primitive archaedictyon the cells (areoles) are irregular in size, form and arrangement.

Stubs of crossveinlets are often seen projecting into the larger cells, most often in the more primitive Anisoptera, as if in the process of reduction. That these stubs are residual in character, not progressive as Tillyard implied, is indicated by their crudeness of form and inconstancy of occurrence. They do not have smoothly rounded growing points, as do developing nerve endings in flesh and root tips in soil, but are blunt-tipped, rough, and obviously superfluous. Bits of unreduced archaedictyon persist even in such well-defined areas as the midbasal space of *Boyeria* and other primitive Aeschnids, and in the male basal triangle of such Gomphids as *Gomphus vulgatissimus* and *Ophiogomphus aspersus*.

Differentiation and reduction have gone so far in Odonata that it is only in the wider interspaces of the wings of large species that one finds hexagonal cells in regular rows. Between closely neighboring veins they have become quadrangles; between veins a little wider apart, two rows of alternating pentagons (one angle gone from each); or, if veins be still wider apart, then a row of hexagons between two rows of pentagons—a beautiful adjustment widely prevalent in many Libellulinae. If there be space for additional rows of hexagons, each additional row will generally be introduced by a single pentagon, that presents an entering angle to fill the space between two rows and a flat side to succeeding hexagons.[13]

Areas of clearance of crossveins occur in different parts of the wing with developmental divergence, but generally around arculus,

[13] This I have illustrated in my "Genealogic Study," 1903, p. 751. A chaotic state of crossvein reduction is seen in the wing fragment of the very aberrant fossil, *Aeschnidiopsis flindersiensis*, as figured by Tillyard in Proc. Linn. Soc. New S. Wales, 42: plate 43, 1917.

triangles and paranal cells. Perhaps most general of all is the clearance of superfluous antenodals from both ends of the Costo-Radial. This particular clearance is most extensive in Zygoptera, where but two antenodal crossveins are retained in all the higher members of the suborder.

In the families of Anisoptera whose males have developed a basal triangle one may follow the course of specialization by counting the cells within that triangle: numerous in a few primitives; becoming more or less stabilized at three cells in Gomphines, at two in Cordulines, and reduced to a single cell in genera of small stature. Noteworthy clearance of crossveins from the intermedian space appears to be confined to the higher Gomphines. Similarly, clearance of postnodals from both ends of the second postnodal interspace marks special progress in Libellulinae.

There has been a progressive expansion of the anal area of the hind wing in the Anisoptera. The inner margin of this area is so greatly widened in higher Libellulinae, such as *Pantala, Tramea* and *Celithemis,* that the upper surface of an outspread wing is not all visible from above, the inner margin being turned downward to a vertical position alongside the base of the abdomen. This breadth seems to have imposed new difficulty at the time of transformation. Not infrequently one may find a dead nymph held by a wing that could not be withdrawn; I do not recall ever having seen a Zygopteran so held.

In Retrospect and Summary.—The study of the relations between tracheae and veins in dragonflies is not new. It appears to have been begun by Dr. H. A. Hagen 104 years ago, when he published a paper about a page in length, entitled: *Ueber die Bildung des Geaeders/der Libellenfluegel.*[14] In this he wrote:

"By simply rubbing the expanding wing of a transforming dragonfly nymph between thumb and finger, the two membranes of the wing may be slipped apart, and it will readily be seen that the venation is double; i.e., developed alike in both membranes, and that the double network thus formed is united and exactly coincident along the course of the wing tracheae."

Thus early he showed that the two chief elements of the dragonfly wing are the air tubes within and the hypodermis, with its

[14] Hagen, H. A. Stett. Ent. Zeit., 7: 115-116, 1846.

cuticle, without; and that these together form the venation pattern.

Before Comstock's time, in the days when each order of insects had a vein notation system of its own, different from all the others, there had grown up among students of Odonata a set of names for veins that answered the requirements of the time very well, and that was quite consistently used by Hagen, de Selys, Brauer and others. When de Selys, with Hagen's close cooperation, used that system in his classic *Monographs* and *Synopses*, it became well established. In order to read these classics, every serious student of Odonata must know the old names for veins as well as their modern equivalents. (See also text-figure 5, page 37).

All the long veins of the wings behind vein R1 were called sectors; in order from the front they were:

de Selys	*Comstock*	*Tillyard*
Principal Sector	M1	R1
Nodal Sector	M2	R3
Subnodal Sector	Rs	IR3
Median Sector	M3	R4 + R5
Short Sector	M4	MA
Upper Sector of Triangle	Cu1	CU2
Lower Sector of Triangle	Cu2	A1

The last two spring from the hind angle of the triangle. Their names tell their placement in the wings of the more generalized Anisoptera. The other sectors all trace proximally to the arculus, where they are based on two divergent stems called the *Sectors of the Arculus*—a goodly name that is self-explanatory and well worth keeping for modern use. It is more convenient than are the names that speak in terms of homology:

de Selys	*Comstock*	*Tillyard*
Upper Sector of the Arculus	M1 + 2 + 3	M1 + M3 + IM3
Lower Sector of the Arculus	M4	M4 + 5

This is perhaps as good a place as any to relate how the vein names of our "uniform system," selected by Redtenbacher and adopted by Comstock, came to be applied to Odonata.

From the time of Dr. Hagen's study in 1846, tracheation seems not to have been investigated again until 1888, when Brauer and Redtenbacher published a photograph of the nymphal wing of a

species of Aeschna.[15] It showed by transparency tracheae and veins together. Is was much like our photograph reproduced herewith as Plate III, figure 2.

In 1896 Professor Comstock, who was alert to everything that promised new light on his main life-problem, insect-wing venation, brought the copy of the *Anzeiger* containing that picture into the laboratory where I was working under his direction, as a graduate student. Because I was then collecting and rearing dragonfly nymphs, he suggested that I bring in a living nymph and mount a wing from it for him to photograph. Thus began our work together on dragonfly-wing venation. Out of it grew, first the Odonata Chapter of our joint series, *The Wings of Insects* (Amer. Nat. for 1898 and 1899) and later my own *Genealogic Study* of 1903. It was the study of tracheae that first cleared the way for a logical application of the Uniform System to Odonata.

Soon after the publication of my work Tillyard took up the task in Australia, first verifying my results and then advancing our knowledge greatly by his studies of tracheation in the more primitive Australian and New Zealand species. He published a long series of brilliant contributions to knowledge, as hereinbefore noted.

And then he abruptly discarded it all, and adopted with too much enthusiasm Lameere's beautiful, blue-sky fluting theory. But the tracheae are still present and they speak for themselves. Veins still form about them. Their pattern is still the basic pattern of every Odonate wing.

I have found tracheae, far from being a "will-o'-the-wisp," to be substantial, and very dependable as to their general behavior. They stay in fixed mutual relations in the nymphal wing. I expect that they will continue to spring from a big tracheal trunk at the wing root. They will be of the number and pattern that characterizes so many insect orders. At first appearance they will stand far apart. As the wing grows they will be crowded together as the formation of the basal hinge compels; and the ones at front and rear, where pressure is greatest, will be more or less crowded

[15] Ein Beitrag sur Entwickelung des Fluegelgeaeders der Insecten, Zool. Anz., XI, pp. 443-447.

out. Those toward the middle of the wing, being more favorably situated in relation to air supply, will reach out and occupy and fill with their branches the growing wing tissue. The long tracheae will at first be more or less parallel and loosely extended in the flat hypodermal sac, like one's fingers in a mitten. As the veins develop around them, they will be shut in, like fingers in a glove. They will become crowded more and more closely together just beyond their still separate bases. Veins R and M at the front, and Cu and A at the rear, will become bound together in pairs for a distance, so completely that they will appear in the adult as single veins. There will be the basal bendings of two main tracheae, and both losses and gains of their terminal branches, as hereinbefore detailed; but the adult venation, laid down before these losses and shiftings occurred, will develop along the original lines as vein formation becomes dominant over growth. It is no wonder that the complexity of the adult venation was baffling until its ontogenetic history was made known.

Viewed in the large, no great insight is needed to see that two primeval peculiarities of Odonate tracheation have provided the most constant structures in the wings of the Order:

1. The crossing of trachea Rs in the beginning provided the foundation (*Sn*) on which was built the middle (nodal) tie-up of the veins of all true Odonata.

2. The forward shift of the Anal trachea, and its return to its original level from contact with trachea Cu *via* the anal crossing (*Ac*), left that crossing also a distinctive mark of the Order.

Whatever gains in area of the hind wing in Anisoptera, or whatever losses in area near the base of both wings in Zygoptera, may have occurred, these two strong points of support, *sn* and *Ac*, remain fixed and distinctive.

If there was earlier a fluting of the wing surface, these cross-linkages superadded to it, or in part replacing it, provided the wings with a better supporting framework. They probably favored differential strengthening for more efficient service in flight.

Insects that have no special cross-linkage of the long veins of their wings (mayflies and termites) use their feeble wings for their one mating flight; one flight in a lifetime, and wings are no longer needed.

The tracheae of larvae are of little help toward understanding the venation of the adult in the holometabolous orders of insects (those without a pupal stage). They serve fairly well in the lower Neuroptera and Lepidoptera; not at all in the Diptera and Hymenoptera. There is a reason for this.

In larvae, wings develop internally with infolding of the skin, and they are covered by overgrowth of it. Thus the wings are hidden beneath the surface and not visible from the outside during the larval period. But each wing is still essentially a simple hypodermal sac, a very small one, called an "imaginal disc," or more simply, merely a wing bud.

Wings are retarded more and more in their development as specialization proceeds. In most larvae of insects the wing buds are so small that *tracheoles* are long enough to deliver the needed ozygen; and so tightly compressed are they that *tracheae* do not get inside until, as transformation approaches, the folds begin to be released. Vein development does not wait, however, but proceeds after the early ancestral pattern: principal veins in the same sequence and relations, only varied in shifts, fusions and consolidations of parts, each order shaping them after its own patterns.

When release comes to the wing buds, the tracheae may either enter the veins, as in Lepidoptera, or may not, as in Diptera. "Imaginal discs" explain why tracheae are of no aid in determining homologies in the higher Holometabolous Orders.

Nothing was made more clear by Comstock and myself in our joint papers, *The Wings of Insects* (Amer. Nat. 1898 and 1899) than that tracheae tend to be reduced with increasing specialization. This is true throughout the orders, and within each order studied, throughout the families. We searched developing wings of whatever genera were available for signs of primitiveness, and always found the fullest complement of tracheae associated with the greatest likeness to the more primitive members of other orders and families. Thus they showed the "convergence backward" that is the surest indication of the direction that evolution has taken.

After Tillyard.—Tillyard found Lameere's version of Adolph's wing-fluting theory very much to his liking; and so have others ever since Adolph's time.

Lt. Col. F. C. Fraser, foremost of Tillyard's disciples, rushed in to adopt the Tillyard system, even before it was fully developed; and he has continued to be its most ardent supporter. He hailed it as a great gain. He wrote (Jour. Bombay Nat. Hist. Soc. for Aug. 1, 1927):

"It now brings the dragonfly venation into line with other orders of insects [!] and is certain to be adopted in the future" [!!]

But Fraser has latterly been digging a little more deeply into the subject of venation. He has wholly renounced Tillyard's misplacement of *Hemiphlebia* with the Calopterygidae.

In a notable paper on the origin of the nodus in Odonata he has found evidence that the subcostal vein, which swings forward at its tip and seems to end at the nodus, once continued outward along the front margin of the wing. The evidence is in the vestiges of a vein that once followed that course. There is still to be seen on the under side of the nodus a flat, cuticular ridge, that once, as an open channel, enclosed a longer subcostal trachea, and that still marks its former course; a vestige merely, in process of disappearing.

This explains why the costa, a high vein, appears as a low vein beyond the nodus in dragonflies. The costa has disappeared there as a separate vein, and in the course of that disappearance the subcosta, a low vein, has taken over and has gradually reversed the fluting.

This replacement idea is supported by certain facts of nymphal wing development in Odonata. The wing pads lie inverted upon the back with costal margin of both fore and hind wings uppermost. In this position the costal edge is exposed to abrasion by whatever may be loose in moving water. In the course of the ages the most exposed half of the costa has been battered out of existence; or rather, has been crowded back and consolidated with the subcosta.[16] Perhaps it was out of a residuum of vein-making substances that the stigma was fashioned.

Of all insect nymphs known to me, only those of the jumping Orthoptera have the wing pads lying upside down upon the back.

[16] Wherefore, happily, we still may properly call the resulting single vein the Costa.

Perhaps it is more than a coincidence that the Orthoptera and Odonata have costa reduced, and radial sector reduced, and the area of the median vein enlarged.

Nature has provided the back of the nymphal abdomen with a row of bumpers, called "middorsal hooks." These hooks are largest and strongest in those nymphs that live upon the bottom of streams and on wave-washed shores, where gravel and sand are tossed about in the water. In some stream-dwelling *Macromia* nymphs, the tops of the dorsal hooks are battered and flattened as if by abrasion. They may be taken as evidence of rough treatment received during the ages, and may account in part for the recession of the Costa and its consolidation with the Subcosta—again, the "impress of environment".

Fraser also noted the looseness of the proximal end of the bridge where it turns forward in most Odonata, (backward in a few, mostly fossil forms) to make contact with vein M within the middle fork (Mf); and by a masterly piece of circumlocution seems to have convinced himself that this looseness should not be considered evidence of the secondary nature of the bridge! (Proc. Roy. Ent. Soc. London, (B) 13: 58-67, 1944.)

Fraser has strayed so far from the Neo-Adolphian fold as to be willing to look at wing tracheae. And looking at the Anal trachea, he has seen that its circuitous course forward against and along the cubital trachea and back again down the anal crossing to the original level, is but a detour, its former road being blocked by pressure from the rear. And he has seen that the crossing, Ac, has added an enduring element of strength to the wing base. He writes:

"*The phylogenetic importance of this short cross nervure Ac cannot be exaggerated.* Its presence in modern Odonata shows not only the path the anal trachea has taken, but also shows that the base of the wings has at one time gone through a process of great reduction, the process having been responsible for driving the trachea inward."

This statement is good morphology.

Dr. V. Martynov published in 1922 a dissertation that should be mentioned in passing (Rev. Russe Ent., 18: 145-174. Translated for publication in Psyche, 37: 245-281, 1930, by F. M. Car-

penter). Its title was "The Interpretation of the Wing Venation and Tracheation of the Odonata and Agnatha" [Ephemeroptera]. Its purpose seems to have been to prove the unreliability of evidence from tracheation. He selected as a basis of his brief discussion of tracheae the order Ephemeroptera; an order that is very highly specialized in its own way, and that has its own peculiar mode of tracheal reduction. He added no facts, but based his statements wholly on the excellent figures of tracheation that were published in 1912 (Ent. Soc. Amer., 5: 89-106) by Dr. Anna H. Morgan. He then devoted two paragraphs to tracheation in Odonata. He says that he collected four specimens of a species of *Aeschna* and studied the tracheation of their wings, and found it freakish in one of them. He made that one the basis of a labored argument to prove the inconsequentiality of all evidence from tracheae. I do not doubt the correctness of his presentation of the aberrancies of that one nymph, though I have never seen anything like it—trachea M4 separated from M1-3 back to the very basal tracheal trunk. I have seen other occasional departures from the normal tracheation. They are to be expected, and do not appear to occur more often in tracheae than in other organs, and should not be more disquieting. His discussion ends with this summary (quoted from Carpenter's translation):

"And so the investigation of the tracheation of the wings of dragonflies and mayflies from a functional and historical point of view leads us to the conclusion that the peculiarities were developed in connection with the acquisition of the characteristic features of these groups, the alternation of convex and concave veins, and usually the change of the convex ones into 'inserted sectors.'" [? ? ?]

It is evident that he did nothing with tracheae worthy to be called an investigation, or even a careful inspection.

Dr. Clarence H. Kennedy was another faithful follower of Tillyard. He accepted Lameere's revision of Adolph's theory and took the little fossil, which is his namesake, to be ancestral in the order Odonata. He arranged the penes of Zygoptera in Tillyard's support, by aligning them in short evolutionary series, which, like many other series, may be read two ways, either up or

down. To me it seems that he and Tillyard read their evolution series for Zygoptera in reverse.

A recent contributor to the discussion of Neo-Adolphism is Dr. W. T. M. Forbes (Amer. Midl. Nat., vol. 29, 1943). He finds a hierarchy among the flutings of the wing surface; "four special plaits" (*l. c.*, p. 396) where two veins of opposite sign (+ and −) run closely parallel for a distance with usually only a single series of cells between them (my own "paired veins"). He affixes no + or − signs to any of his numerous figures; he makes no mention of *Kennedya;* but he agrees with Tillyard in explaining away Rs by calling it a "tracheal specialization," and he does it with an equal indifference to lack of evidence. He suggests that veins Sc and M may be low veins because muscles attached to their bases have pulled them down, so to speak.

Forbes presents a new application of Neo-Adolphian theory in a system of his own, expressed in a table of comparative vein-nomenclature, and he gives labels at both base and tip of all the long veins. Compared are three systems: his own, Comstock's and Tillyard's. The vein labels get another shifting; behind vein M1 none are in agreement with either of Tillyard's systems. Thus confusion is worse confounded.

No two Neo-Adolphians seem to quitė agree on vein labeling. Recently Borror, with Kennedy at his elbow, had to consult still another Neo-Adolphian authority as to where to stick on his vein labels (Ann. Ent. Soc. Amer., 38: 168, 1945).

Now we have Adolphian systems proposed by Lameere, Tillyard (two of them), Martynov and Forbes, with vein labels exchanging places as readily as a catbird shifts from perch to perch. They should all be permitted to rest peacefully in the welter of speculation and argumentation that has accompanied their birth.

Concluding Remarks.—All future students of Odonata will find Tillyard's long series of papers published in the Proc. Linn. Soc. of New S. Wales during the years 1915-1925 a rich mine of facts on Odonate structure and development; facts clearly stated, such as any one can easily verify for himself; contributions to knowledge that were only marred by his constant effort to make the veins of the adult forever conform to the tracheae of the nymph. In his later work on fossils, there is seen the same painstaking

care in his drawings, but it is accompanied by a most arbitrary interpretation of relationships. His wildest guesses were announced with the certitude of an oracle, and have been taken by some of his colleagues as flashes of genius.

Tillyard's diligence in the discovery of facts and his skill in presenting them are admirable. His ever-changing interpretation of the facts is regrettable. His passion for renaming things is ludicrous: "Italian loop" for the foot-shaped anal loop of the Libellulinae, for example; Ax and Px for antenodal (*a. n.*) and postnodal (*p. n.*) crossveins—new, arbitrary symbols that carry no clue to their identity and location; "Agriidae" for Agrionidae and its derivatives; names far less euphonious, and that render the source of the many Agrion-names less evident. This change is uncalled for, and a clear violation of priority.

He went over to paleontology, bag and baggage, and only returned to add a few more names. What a Field Day he must have had when naming 15 new subfamilies of Libellulidae,[17] where three had sufficed before, without adequately defining any of them!

He turned for relief to the field of Paleontology, where tracheae cease from troubling and competent critics are few and far between.

The Tillyard System has been developed in my time and I have studied it diligently. I knew Dr. Tillyard personally very well. He was a valued correspondent of mine to the end of his life. We exchanged papers, and I think I have read all that he wrote about dragonfly-wing venation. His factual contributions to the knowledge of the order are hardly exceeded by those of any other Odonatologist. But when he rejected all evidence from ontogeny and fled to a theory of alternating convex veins as basic in insect phylogeny I could not go along with him.

Tillyard left behind him a system that does not make sense, encumbered by vein-labels so bungling that his own followers get confused in using them. Especially troublesome is his whimsical "IR2a," now "IR3" (a nuisance to typists and compositors as well).

[17] A feat that was surpassed only by C. H. Kennedy when he named 42 hitherto unrecognized new genera and subgenera of Zygoptera (Ohio J. of Sci., 21: 88), defining most of them by their penes only. Most of them hang by their penes still.

The Comstock System presents no such difficulties. It abides by the facts of ontogeny and traces the veins from their sources. It has no theory to promote; sticks close to facts that anyone can verify from material that is everywhere available; is consistent throughout and easily understood; and leaves the student with a feeling that his feet are on solid ground.

Abstract

This paper outlines the plan of a new Manual of the Dragonflies of North America that is now in manuscript, and discusses its practises: making of keys and tables, naming of thoracic stripes and sutures; placement of wing venation figures and systems of notation of wing veins, with special attention to the Tillyard System in Odonata; recounts the origin of that system and the repeated changes made in it. It ends with an extended discussion of insect wing venation in general and, more particularly, with that of the Order Odonata.

Explanation of Figures

Plate III

Fig. 1.—Photograph of a nymphal wing of *Cordulegaster obliquus*. In making this preparation the rearward extension of the large tracheal trunk was cut off at the base of the Anal trachea. The basal hinge of the adult wing will form between the slight notches in the margins of the wing sheath at h—h. The field of the weak and distant Costal trachea (C) is being taken over by accessory branchlets that spring forward from the Subcostal trachea. The anal field (A) is as yet traversed only by transient tracheoles. X is a side branchlet that does not enter the wing.

Fig. 2.—A hind wing of a nymph of *Anax junius* in the penultimate instar. Note the lack of arculus, the faint indication of triangle and of stigma, and the partly developed bridge. The anal loop is foreshadowed by the course of the trachea A1, which bounds it on three sides. Note that the formation of the two planates *Rpl* and *Mpl* is begun without benefit of any antecedent tracheae.

This particular nymph was nearing a molt, as is shown by the contracted edges of the wing margins within the loosened wing sheath.

Photograph by Dr. M. J. Westfall, Jr.

Plate IV

Photographs of nymphal wings showing tracheae and veins together. Above, fore and hind wings of *Anax junius*. Below, the same of *Tramea lacerata*.

Plate V

Wings of *Anax junius*, male, lighted to show flutings and other unevennesses of the surface. Note the cross-fluting of the areas where the radial and median planates are developed. Crossing these planates are accessory tracheal branches from the rear side of veins Rs and M4.

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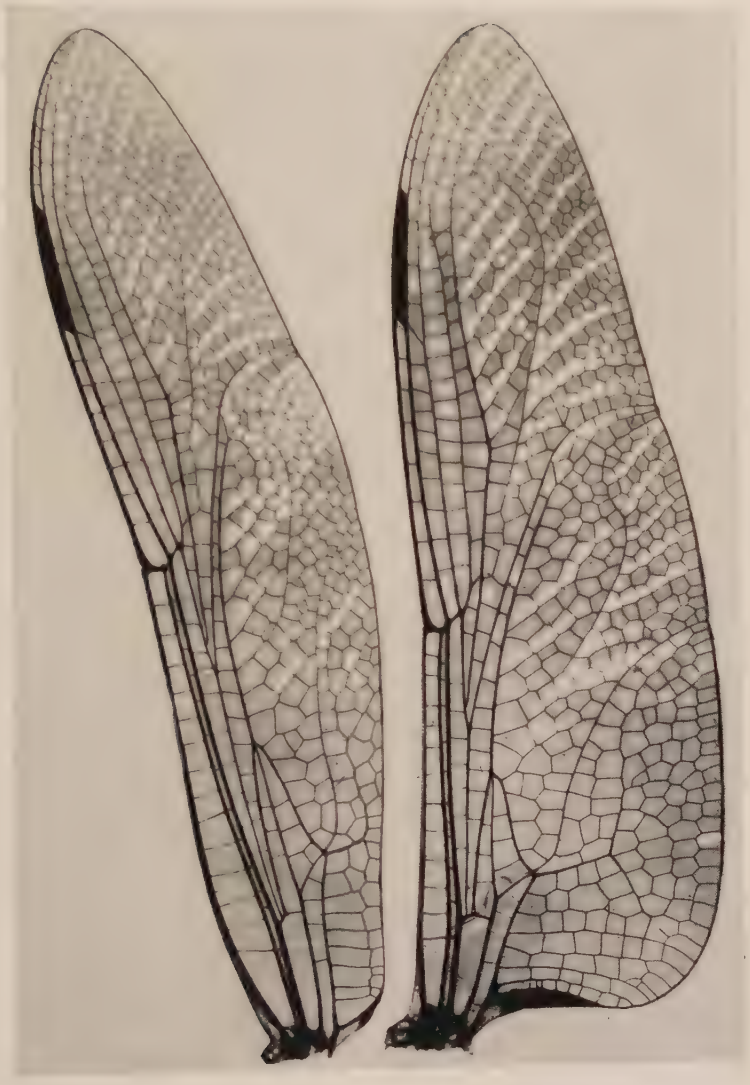

NEEDHAM—PRODROME FOR MANUAL OF DRAGONFLIES

DISTRIBUTION OF SPHINGIDAE (LEPIDOPTERA: HETEROCERA) IN THE ANTILLEAN-CARIBBEAN REGION

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Introduction

If one were to do a wholly satisfactory piece of work on the distribution of Sphingidae (hawk moths) in the Antillean-Caribbean region, it would entail months, even years, of residence in the Lesser and Greater Antilles, Trinidad, Venezuela, Mexico, Central America and Florida. One must have collected all the species in each country, reared many of these, made a thorough study of the geographical barriers, of climate, humidity, temperature, food plants and predators. In one lifetime this would hardly be possible, even if one lived no normal life outside of this study. Although I include all of these regions in this report, I have concentrated on collecting in, and observations on, certain of these places myself, and have called on the knowledge and experiences of other collectors and observers for other sections. I have worked especially in southern Florida, in Jamaica of the Greater Antilles, in Venezuela and Guatemala. Although Florida is not a Carribean country, it is quite impossible to tell where the Caribbean Sea ends and the Atlantic Ocean begins, and a home base as a standard of comparison is really essential. Jamaica is probably one of the oldest of the Greater Antilles; it is a smaller island than Cuba, its mountains and seacoast are in close proximity, it has been isolated for so many geologic years that its sphingid population has a definitely insular character, and it has the Hope Gardens near Kingston. Here, the magnificent beds of bright, fragrant flowers attract hundreds of Sphingidae at dusk—species coming from both mountains and seacoast—often traveling long distances to this unparalleled supply of nectar. I have chosen Venezuela among the South American countries because it has the longest Caribbean coast line,

this coast line supplying mountains in the Coastal Andes, humid, tropical lowlands in many regions such as Ocumare, and a magnificent primeval Cloud Forest, unspoiled by man. Trinidad is selected because it is an island very near to the South American continent and especially to Venezuela, knowing that it will be of significance to discover whether the majority of Sphingidae found there are South American or Antillean in character. Mexico and Central America have long Caribbean coasts and are of special interest because of the meeting there of North and South American forms.

This report is based on personal observations made in field expeditions to the countries under consideration. I think it may be true that more learned treatises are written by scholars who bury themselves in their laboratories, and who are so engrossed in the purely taxonomic side of entomology that they have little time for any actual, vivid, living confirmation of their work or extension of its bounds through experience in the field itself. There seems to me, however, to be a stamp of authority given by one's own observations and work in the field, that can come from no other source.

Of the many trips I have taken to Florida, I think of three as especially outstanding in results for this report. These trips were taken either with Mr. Cary or my nephew, John W. Cadbury, who is also an entomologist. In late March, 1924, we spent some time collecting at Everglades City on the west coast which is much less man-spoiled than the east coast. On this particular field trip we happened to run into a virtual nest of two scarce species, *Madoryx pseudothyreus* and *Phryxus caicus*. Although we returned several times it was not until April, 1946, that we had another prize collecting experience there. This time, among many scarce species, we secured *Protambulyx carteri* and *Phlegethontius brontes cubensis*. Another time my nephew spent three months near Florida City, sugaring, collecting at night, and rearing some of the Florida Sphingidae. Mr. Cary and I spent some weeks collecting in Guatemala and we have twice spent long periods in Jamaica. In June, 1949, John Cadbury and I spent four weeks collecting in the Cloud Forest of Venezuela at Rancho Grande. We have done much field work in the Okefinokee Swamp in southern Georgia, and at

Map 1. Antillean—Caribbean Region of this Study.

our summer home in New Hampshire we have successfully bred, and recorded descriptions of all stages of, the Sphinx moths found there. We have collected extensively in the Sierra Nevada and in the Rocky Mountains and have had one successful trip at Caesar's Head, South Carolina. In this way we know what to look for in the field, how to find necessary food plants which we would otherwise miss, and we know a good locality when we see one. We have found that where the flora is varied and rich, insects abound. During all these years we have kept accurate and detailed records. All of this preliminary training led me to undertake this rather ambitious piece of study on the distribution of Sphingidae in the Antillean-Caribbean region. I know that my extensive field work has sharpened my powers of observation, enabling me to understand the general ecology of each place and to interest myself in the intricate relationships of climate, altitude, temperature, humidity, prevalence of parasites or predators. When we are in the field my nephew and I concentrate wholly on the work in hand, sleeping very little, collecting until all hours of the night, and studying the flora and fauna by day. In this way, much can be accomplished in a short time. Notes taken in the field fall into shape in long hours of working over them at the home base, while one lives one's normal life in the family.

I have chosen the family Sphingidae (hawk moths), not only because of a lifelong interest in them, but also because they are strong flying moths, easy to collect at lights or over flowers at dusk, and because they are large enough and effective enough to show visual differences to the naked eye. The shape of their long bodies and slender wings adapts them to a highly developed air life. Their eminence in flying power has led to an extensive geographical distribution with suitable adjustments to climatic conditions and occurrence of food plants for their larvae. They are more numerous in tropical and subtropical countries and become sterile in the cold regions of the far north. If extensive, deserts may become impassable barriers. For example, Mexico is divided north and south by a desert and because Sphingidae must have the nectar of flowers for food, and water to drink, only twenty out of a possible two hundred and fifty species can cross this barrier. They are of course known to have flown much greater distances when provided with food and drink. Dr. Miles Moss, in his

Sphingidae of Peru,[1] says of the handsome *Pholus labruscae:* "Both sexes undoubtedly fly over the Andes from the Interior, where alone the food-plant of the larva, a species of *Ampelopsis,* grows. It is little short of marvellous how this delicate green moth can fly so far, and yet, in the majority of cases, arrive in perfect condition. I saw a specimen intercepted in its westward flight by the lights of Cerro de Pasco at 14,000 feet, while another was taken in perfect form on the shore-rocks of Ancon, twenty miles north of Lima, and far removed from the limits of vegetation." Those species with a wide distribution are generally strong fliers, feed on a common food plant or are more abundant because of a greater freedom from parasites.

In the introduction to their "Revision of the Lepidopterous Family Sphingidae" the authors, Rothschild and Jordan,[2] make some valuable suggestions that should be in the minds of all students of the causes of distribution of the Sphingidae. They point out that a country must be accessible to a species and that no species has been able to cross the Atlantic, the Pacific, the Indian Ocean, or the Sahara Desert. On the other hand, there is no such barrier to prevent *Phlegethontius kuschei* from passing from Mexico to Venezuela, no wide desert to restrict the genus *Orecta* to Brazil and Argentina, no high mountain range, desert, or water barrier that restricts *Sphinx lugens* to Central America, *Sphinx chersis* and allies to North America. "The range of these Sphingidae is restricted because the conditions of life (temperature, food, composition of fauna, etc.) are not suitable outside their present range. It is therefore evident that the limits of the range of a species are determined by two kinds of factors: physiographical barriers, beyond which the species is physically prevented from going; and biological barriers, beyond which the species is not able to exist." Because in this report I shall quite naturally dwell at some length on geologic evidence, I want at this point to emphasize strongly the final point which Rothschild and Jordan make concerning the distribution of Sphingidae. ". . . . it is erroneous to conclude that the limits of the range of species indicate always

[1] Trans. Zool. Soc. of London, vol. XX, part 2, April 1912, p. 105.

[2] Novitates Zoologicae, vol. IX, Supplement, pp. cii and ciii, 1903.

that a physiographical barrier has formerly existed, that there was in the Continent or chain of Islands a discontinuity barring the way. One has to carefully discriminate between those facts of geographical distribution which allow of conclusions being drawn as to the former configuration of the earth's surface and those facts which are the result of the action of biological causes." [2]

Over this wide area (Antillean-Caribbean region) of oceanic islands, the southern end of one continent and the northern end of another continent, Mexico and Central America, there is a number of species that occur in all these regions. Where the same species does not occur we sometimes find the genus represented by another species. Trinidad, South and Central America are more tropical than Mexico, Florida and the Greater Antilles. Into these warmer regions there has been infiltration from the south, while into Florida and North Mexico there has been infiltration from the north. There is in the Antilles probably a certain amount of migration from Central America and from island to island going on all the time. Especially is this true of strong-flying species or at times of hurricanes. Our study deals with the probable causes of the wide distribution of similar species, subspecies, varieties, and in some cases of similar genera in this extensive area. Of special interest in this report are the subspecies and varieties which in some cases replace the species. We are also concerned with those species occurring in only one or two of the localities of the study and with all endemic species. Table No. I shows the species or genera occurring in all five or at least three of the regions, and here the close relationship between Venezuela and Trinidad is at once apparent. Table No. II shows the Sphingidae endemic to each of the five regions, and Table No. III shows the Sphingidae endemic to the Greater and Lesser Antilles. Table No. IV illustrates the depauperate sphingid fauna of the Antilles as compared with Mexico, Central America and South America (no subspecies listed on this table). The Antilles have been so long (in geologic time) separated from each other or the continents, or have been truly oceanic in origin, that a number of species and many subspecies occur only on these islands. The most interesting study by the Academy of Sciences of California of the Sphingidae of the Galápagos Islands,

and the subsequent classification of the genus *Phlegethontius* (*Protoparce*) on the Galápagos, by B. Preston Clark, have contributed much to the study of the origins of Sphingidae on oceanic islands and this will be referred to in a section of this report. James Bond's study, "The Distribution of the Bird Fauna of the West Indies," (revised 1948) has been of great interest and suggestiveness, always remembering that while Sphingidae, like birds, are strong fliers and have been known to fly several hundred miles over water, they are limited in their distribution by their necessity for frequent food and drink and by the presence of food plants for their larvae. This very generalized and brief introduction will serve as a starting point for more detailed study.

Life History of a Typical Sphingid Moth

Perhaps the first paragraphs of this more detailed study should deal with the development of a typical sphinx moth from the shining, round, green egg laid singly on the underside of a leaf of its favorite food plant, through its larval period with its usual four moults, its quiet pupal stage, generally passed underground, to its imago or winged stage. For this special study I am choosing *Phlegethontius sexta*, the common and widespread tobacco moth. Since this moth is found practically everywhere tobacco has been introduced and is common in the Antillean-Caribbean region, I think its life history is interesting, not only for this species but because almost all Sphingidae have a similar development.

The female moth lays her round, green egg, about pin head in size, on the underside of a leaf of a healthy tobacco, tomato, or some plant of the Nightshade family such as Jimson Weed, usually singly, though occasionally in pairs. The egg hatches in about seven days, turning yellowish before the tiny larva breaks through its egg shell. These are small yellow caterpillars about one-eighth inch long, and have a straight reddish caudal horn. Sphinx caterpillars nearly always have a caudal horn of one kind or another in some stage of their larval life. Some have long curling ones, losing them in a later moult, but *sexta* keeps the horn till the pupal stage. The tiny, slender larva eats its egg shell and then eats small round holes in a fresh tobacco leaf. They soon grow green with a white subdorsal line from head to horn. After four days the

larvae stop eating, fasten themselves with a thin web to their food plant and shed their skins. The head falls off like a false face and the skin splits. This is a ticklish process for the young larvae and many die, although for a relatively smooth Sphinx worm, shedding the skin is easier than for one with spines or tubercles. Often as the little worm waits quietly for his skin to split he is attacked by a tiny wasp or Ichneumon fly who lays her eggs in the worm at this time when he is especially weak and unable to defend himself by tossing his head angrily as he does in later stages of his life. The horn is now dark brown, thicker at the base, and white obliques appear, crossing the sub-dorsal line and almost meeting on the back. These larvae usually eat their cast-off skins, though this is not a universal habit. In three days there is a second moult. The head is now round, green with white granules. The body is green with white granules on the thoracic segments and white dots on the abdominal segments. The white obliques are now edged above with black. The anal plate is edged with yellow. In four days there is a third moult. The head is now finely dotted with white. The dorsum is now a white green, the sides very yellow green and the ventral side blue green. The true legs are now green and black. The skins are shed for the fourth and last time in about seven days, and in this last moult may assume different color forms, all the way from white green to almost black, but their marking remains quite similar, with the obliques edged above with black.

They feed now for about ten days. Usually they eat mostly at night, resting at the bottom of stalks or under leaves by day, but if a larva continues eating by day as well as night, is unusually nervous and has droppings that are not hexagonal or regular, it is an indication that it has been stung by an Ichneumon. Before long, the skin is punctured in many places and tiny Ichneumon larvae, which have been fastened to the host's intestine drinking the plant juices, come out on top of the skin, fasten themselves to the *sexta* larva (now about four inches long), spin their tiny cocoons and the poor host crawls around, his back covered with perhaps a hundred rice shaped cocoons. Usually the *sexta* larva is now so weak that it becomes limp and dies, leaving its empty skin hanging with all the tiny cocoons. If, however, the *sexta*

worm has escaped being parasitized, it begins crawling around looking for a place to pupate, exuding certain liquids from skin and anus. It burrows into the soft earth, fashions an earthen chamber, lies dormant, shedding its larval skin in seven or eight days and turning into a brown pupa with exposed tongue case like the handle of a pitcher. If disturbed by any mouse, centipede, etc., during these eight days the soft body will be injured and pupation will not be completed. They remain, unless double-brooded, in the ground all winter. In June when the earth is warm they push their way to the surface, the pupal skin cracks and the moth steps out, the body damp but fully formed, the wings mere stubs, which expand in a few hours as the moth hangs quietly to some twig. At first, after full expansion, the wings are limp and weak, but shortly the liquids within, dry, and after some fanning motions the moth is ready to fly. Its life then consists of flying at dusk or by night from flower to deep throated flower for nectar, of mating and egg laying if a female. Sphinx moths like *Phlegethontius sexta* live for several weeks, even months, if not eaten by birds or bats or caught in a gigantic spider web. Some Sphinx larvae weave a thin cocoon among leaves on top of the earth and the moths of the genus *Madoryx* make cocoons on tree trunks. In Caracas, Venezuela, with our friend, René Lichy, we found many of these white cocoons on the trunks of trees belonging to the Bignonia family. The above account with many variations stands for most of the Sphingidae. Some larvae are more parasitized than others, and some will eat only one food plant, both of these things making them scarce.

Fossil Insects and Probable Geologic Time of Appearance of Sphingidae

Dunbar,[3] in his "Historical Geology" (1948), says that the first fossil insects, so far discovered, date from the Pennsylvanian period. He says of these insects that they are of such a large size and of such diversity of forms that a long antecedent evolution is implied. These may yet be found in Mississippian or even Devonian rocks. He says: "Out of 400 forms known from lower and middle Pennsylvanian strata, more than a score exceeded four

[3] Historical Geology, Dunbar (1948), pp. 271, 301, 347, 379, 393.

inches in length, six attained to nearly eight inches, and three exceeded a foot, the average length being about two inches. The largest of all was a dragon-fly type found in the coal-measures of Belgium, which had a wing spread of twenty-nine inches." Most of these insects were of primitive stocks not exactly like any of the modern orders. However, there were cockroaches so large and so numerous that this has been called "The Age of Cockroaches." About 1,000 kinds of insects are known from the Jurassic rocks and among these we find representatives of most of the modern orders—caddis-flies, dragon-flies, beetles, grasshoppers, cockroaches, and termites. Moths and flies also made their appearance at this time. In the Cretaceous, deciduous trees suddenly became conspicuous and among the oldest of these were magnolias, figs, sassafrass, laurels and poplars. Probably in early Cretaceous times insects adapted themselves to feeding upon the nectar of newly arisen flowering plants and thus assumed their important role in pollinization.

The Sphingidae are largely responsible today for the pollinization of all wild orchids and hence probably arose about the same time as orchids developed from the lilies. In the introduction to "Our Wild Orchids," published by Scribner's in 1929,[4] the coauthors, Frank Morris and Edward A. Eames, discuss the evolution from lily to orchid, saying that while "the lily is famous for simple grace and symmetry" the orchid is noted for fantastic and bizarre shapes. Yet both are modeled on the same plan of a "three-parted flower." To make a long and complicated story short, it was imperative for the developing lily-orchid to tilt the flower on edge so that its face might look outward for visiting insects, and also divide its flower into an upper and lower half. When finally perfected, the orchid has incorporated the inner whorl of three stamens and the middle one of the outer whorl with the style to make a fleshy body known as the column. The lateral pair of outer stamens were made into showy petals closely united with the middle lobe of the corolla which stood between them. This made a landing stage for smaller insects; but, of course, the long-tongued Sphingidae need no landing stage. A nectar well was sunk in the column and the anthers and stigma

[4] Our Wild Orchids, Morris and Eames (1929), Introduction, pp. XII-XVI.

were at the top of the column above the nectary. The great gap between the lily and the orchid from the point of view of evolution is partly filled by two interesting members of our native flora, the *Burmannia* and the *Thalia*. The *Burmannia* is often found in Virginia bogs close to orchids and the *Thalia* occurs in the Missouri marshlands. It belongs to the same order as banana, ginger, arrowroot, but has one showy member, the *Canna*. To attract insects to its scentless flowers, it has turned every one of its stamens into bright petals and its pollen is all stored in a single half anther borne on the margin of one of these stamen-petals. Those who have watched the bees pollinating the lovely yellow flowers of the wild *Canna* in the Everglades will testify that this strategy has been successful.

The evolution of the Sphingidae from those members with short tongue capable of reaching into the florets of a Fringed Orchis to those having tongues from six to eight inches long and capable of reaching deep into the heart of a hanging Angel Trumpet or *Datura*, is a story we know much less well and can only surmise. Dr. Avinoff once saw a great Sphinx taking nectar from a *Datura*, and, quickly squeezing together the bottom of the *Datura* flower, caught the Sphinx by his long tongue, one end of which was in the Datura's honeyed throat.

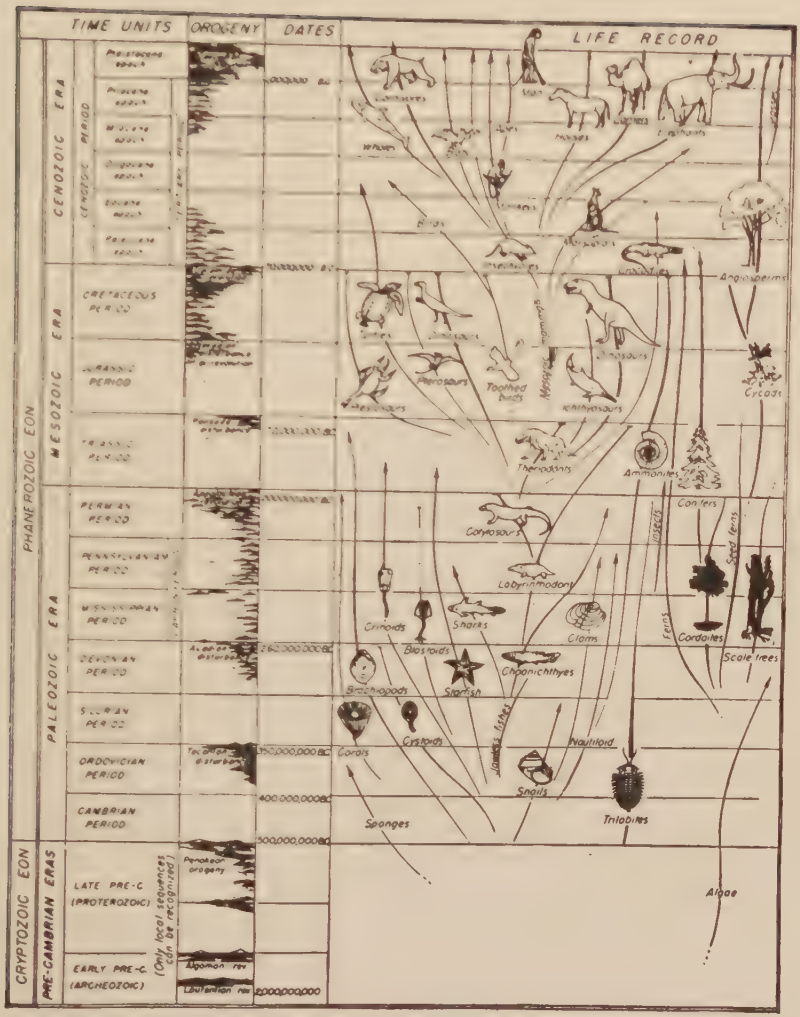
Dr. Walter Sweadner, Curator of Insects at Carnegie Museum, Pittsburgh, and also Professor at the University of Pittsburgh, has illustrated evolution graphically by charts and exhibits in the Museum, and has there a chart showing the probable evolution of insects in which the Sphingidae are among the last to evolve. The situation of the Museum across the street from the University makes it possible for the students to make use frequently of the wealth of material which in so many museums is more or less inaccessible to them. Dr. Sweadner places the evolution of Sphingidae in the Cretaceous, as this corresponds with the evolution of the orchids. So, in studying the distribution of this family, we can quite safely start with the Cenozoic Era. For the benefit of students, who, like myself, have had little geologic training, I append a chart of the Geologic Ages, taken with permission from "Historical Geology," Moore, page 57, and another chart that is very graphic, pictorially, of faunal evolution from "Historical

DIVISIONS OF GEOLOGIC TIME

Eras	Periods	Epochs: North America	Epochs: Europe	Life and other characters	Crustal Movements	Dominant life Characters
CENOZOIC	Quaternary	Recent	Recent	Dominance of man		
		Pleistocene	Pleistocene	Periods of glaciations. Extinction of large mammals	Cascadian revolution	
	Tertiary	Pliocene	Pliocene	Beginning of man		Age of Mammals
		Miocene	Miocene	Culmination of mammals		Age of Modern Seed Plants (Angiosperms)
		Oligocene	Oligocene	Culmination and extinction of archaic mammals		
		Eocene	Eocene	Rise of mammals and modern flores		
MESOZOIC	Cretaceous	Upper: Lance	Danian	Last of dinosaurs pterodactyls large marine reptiles and toothed birds. Last of ammonites. Rise of flowering plants and modern insects. Widespread deposition of chalk	Laramide revolution	Age of Reptiles and Ammonites
		Upper: Montana	Maestrichtian			
			Campanian			
		Upper: Colorado	Santonian			
			Coniacian			
			Turonian			
		Lower: Dakota	Cenomanian			
		Lower: Comanche	Albian			
			Aptian			
		(Absent)	Barremian			
			Neocomian			
	Jurassic	Upper	Portlandian	Rise of toothed birds. Culmination of ammonites. Prolific marine fauna	Jurassic disturbance	Age of Ancient Seed Plants (Gymnosperms)
			Kimmeridgian			
			Lusitanian			
			Oxfordian			
			Callovian			
		Middle	Bathonian			
			Bajocian			
		Lower	Lias			
	Triassic	Upper	Rhaetic	Rise of dinosaurs, pterodactyls, marine reptiles. Rise of ammonites. Rise of cycad like plants	Palisade disturbance	
		Middle	Keuper			
		Lower	Muschelkalk			
			Bunter			
PALEOZOIC	Permian	Upper	Zechstein	Rise of primitive reptiles. Last of trilobites. Glaciation extensive salt beds	Appalachian revolution	Age of Amphibians
		Lower	Rothegende			
	Pennsylvanian	Virgil	Stephanian	Great coal making period. Spread of amphibians. Culmination of spore bearing plants		
		Missouri				
		Des Moines	Westphalian			
		Morrow	Namurian			
	Mississippian	Chester	Dinantian or Culm	Culmination of crinoids. Abundant sharks	Culmide disturbance	
		Valmeyer				
		Kinderhook				
	Devonian	Upper: Chautauquan	Famennian	Rise of Fishes. Rise of landplants, first forests	Acadian disturbance	Age of Fishes
		Upper: Senecan	Frasnian			
		Middle: Erian	Givetian			
		Middle: Ulsterian	Eifelian			
		Lower: Oriskanian	Coblenzian			Age of Spore-bearing Plants
		Lower: Helderbergian	Gedinnian			
	Silurian	Cayugan	Downtonian	Abundant brachiopods reef corals. Salt deposits and iron ore beds	Caledonian revolution	
		Niagaran	Ludlovian			
		Medinan	Wenlockian			
			Llandoverian			
	Ordovician	Cincinnatian	Caradocian	Culmination of trilobites. First appearance of fish like vertebrates	Taconic disturbance	Age of Invertebrates
		Mohawkian				
		Chazyan	Llandeilian			
		Canadian	Arenigian			
	Cambrian	Ozarkian	Tremadocian	Dominance of trilobites. Rise of primitive cephalopod. First abundant invertebrate fossils	Green Mts disturbance	
		St. Croixian				
		Acadian				
		Waucoban				
PROTEROZOIC	Keweenawan			Remains of life mostly lacking. Fossil algae. Iron and copper deposits	Killarney revolution	Age of Sea-weeds
	Huronian	Upper (Animikian)				
		Middle			Algoman disturbance	
		Lower				
	Timiskamingian					
ARCHEOZOIC	Keewatin		Archean	Granitic and schistose rocks complex structure. Only indirect evidence of existence of life	Laurentian revolution	Rise of Invertebrates

From Historical Geology by R.C. Moore. Copyright, 1933; Courtesy of McGraw-Hill Book Co.

Chart 1. Divisions of Geologic Time.



Geologic Time Chart. Ascending lines indicate the range in time of most of the chief groups of animals and plants. If the line ends in a crossbar, this denotes the time of extinction; if it ends in a dart, the group is still living.
Reproduced by permission from Historical Geology by C. O. Dunbar, published by John Wiley & Sons, Inc., 1949.

Chart 2. Geologic Time Chart.

Geology," by Dunbar, page 20, also with the kind permission of the author and publisher. We shall in our study be little concerned with what took place before the Cretaceous and shall be greatly concerned with the geologic history of the Antillean-Caribbean Area in the Cenozoic Era.

Findings of Schuchert, 1935 [5]

In 1935, Schuchert [5] published a volume called "The Historical Geology of the Antillean-Caribbean Region," and since many of his findings are of special interest in this study, I shall give a brief resume of those parts which have bearing on the distribution of Sphingidae in this region. Perhaps the most important is the supposition of the existence of a land bridge, until late Oligocene, connecting Honduras and Jamaica. This would make Jamaica an easy migration route from Central America to the other Antilles. He also thinks it probable that at one time Hispaniola was connected with Jamaica and at the same or another time connected with Cuba. Schuchert is inclined to the belief that the Greater Antilles were broken off from an immensely larger Central America, and are therefore continental fragments rather than oceanic islands. He feels that the separation was probably permanent in the Miocene, certainly so by Pliocene. He thinks that North and South America have been connected by the rising of the Isthmus of Tehuantepec since the Pliocene. He believes that the Pliocene was for the West Indies the time of highest and widest emergence and that the land bridge, or shallow water, between Honduras and Jamaica began to sink permanently in the Miocene when Yucatan and Florida began to be raised.

Schuchert, in discussing the geologic origins of Trinidad, Tobago, and perhaps the Barbadoes, believes all of these to have been a part of the Parian Shelf of the ancient northern boundary of South America (Venezuela). This borderline probably once continued unbroken to the Barbadoes. Since the Parian Shelf of Venezuela did extend so far it is reasonable to ask whether there is any indication of a recognized land migration from the Barbadoes, Trinidad, Tobago, through the string of islands generally

[5] Historical Geology of the Antillean-Caribbean Region, Schuchert 1935, pp. 105-109 ff.

known as the Lesser Antilles, and from them to the Greater Antilles. Schuchert with his meticulous care gives the views on this point of the authorities of many of the faunal groups. He gives much evidence as to the Land Snails, Crayfishes, Prawns, Spiders, Fishes, Amphibians and Reptiles, Birds and Mammals, though touching very lightly on Insects. He feels that the Mammals have left the most positive geological evidence of any of the faunal groups. He feels there is no evidence in faunal dispersal of a land bridge uniting the festoon of the Lesser Antilles with either South America or the Greater Antilles, and that at least as far as Mammals are concerned the faunal life is of waif dispersal (p. 108). There certainly is almost nothing to indicate such a land migration as far as Sphingidae are concerned. However, there is a most interesting instance in a genus of the cockroaches (flightless) which occurs in Martinique and has reached Puerto Rico also. The Lesser Antilles, or Caribbees, are of two quite distinct formations and are generally divided into what might be called the older or limestone, and the younger, or volcanic, Caribbees. To the older limestone division belong such islands as Antigua, Grande Terre, Maria Galante and others. Among the younger volcanic islands are St. Kitts, Nevis, Dominica, Martinique, St. Lucia, St. Vincent, and Granada.

Schuchert says (page 108): "Cuba, Jamaica, Hispaniola, and Puerto Rico-Virgin Islands are each an evolutional center, with most of their individual species endemic, showing that the four island entities had long epochs of isolation during the Cenozoic. Jamaica has the oldest life, or at least the greatest differentiation, and has been longest separated from Cuba; it continued, however, to be connected off and on with southern Hispaniola and with Central America, whereas Cuba remained more or less attached to Northern Hispaniola." On page 109 he says: "The Greater Antillean land faunas apparently also include those of the limestone islands of the northern Caribbees. Both their recent and their fossil life are mostly of the older Antillean stock, and not related to those of the younger Caribbees and South America." These two statements are of significance in the discussion of the distribution of the Sphingidae in these regions and will be referred to in later parts of this paper.

Findings of Bond, Mayr, Darlington, Etc.

Since the publishing of Schuchert's monumental work in 1935 several men have carried forward the study of the distribution of the fauna of the Greater Antilles and have come to different conclusions both as to the geologic origins of the Greater Antilles and the way in which their fauna originated. Among these men are James Bond, author of "The Distribution of the Bird Fauna of the West Indies," 1948, Ernst Mayr, author of "The History of North American Bird Life," 1946, and "Systematics and Origin of Species," 1942, and P. J. Darlington, Jr. who wrote in 1938 an article called "Origin of the Fauna of the Greater Antilles, with Discussion of Dispersal of Animals over Water and through the Air." Since the Sphingidae of this study are strong flying insects and since my study of their distribution in the regions covered in this report bears out the work and conclusions of these men, I incline strongly to their opinion of water and air dispersal as far as Sphingidae are concerned. I feel also that David Lack's study of the Galápagos Finches, published in 1945 and the findings of the expedition of the Academy of Sciences of California to the Galápagos Islands (1911) and the subsequent revision of the "Genus *Phlegethontius* (*Protoparce*) of the Galápagos Islands," by B. Preston Clark, in 1926, bear in evolutionary significance an important relationship to this present study. I shall first refer to Bond, Mayr and Darlington concerning dispersal and shall in another paragraph deal with the evolutionary significance of the work of Lack, Clark, and the Academy of Sciences of California. I shall follow Mayr, 1942, in his "Systematics and Origin of Species."

Bond[6] feels that the bird fauna of the West Indies is "fundamentally and predominantly tropical North American, derived from the north and from the west." We must remember that at the time of these dispersals the climate of North America was certainly much warmer than it is today, and also that tropical North America is supposed to extend to the western part of Panama. He continues: "The South American element, which entered through Jamaica and the Lesser Antilles, is of comparatively re-

[6] Bond, James, 1948, Origin of Bird Fauna of West Indies, Wilson Bull., vol. 60, no. 4, pp. 207-229.

cent arrival and comprises only members of aggressive families." Before the Isthmus of Tehuantepec arose, connecting North and South America, there was a group of islands between the two continents. After this gap was closed in Pliocene time there was a great influx of South American fauna into Central America, and these aggressive forms probably drove out certain birds which took refuge in the Greater Antilles. Ernst Mayr, 1946,[7] thinks that the influence of this joining of the two continents was of immense significance in distribution. He adds further that today few authors believe in "violent upheavals" but tend to believe in the "permanence of continents and oceans" certainly as far as any geologic era influences the dispersal of fauna to the Antilles. Darlington[8] in 1938 gives us clearly his convincing views on the means of dispersal of the fauna of the Greater Antilles as those over water and through the air. Since this very careful study has much bearing on my work on the distribution of Sphingidae in the Antillean-Caribbean Region, I shall give all of Darlington's summaries. He gives four main characteristics of the fauna of the Greater Antilles:

1. It is derived chiefly from Central America with some N. American infiltration.

2. The fauna is fairly homogeneous and very orderly. The islands, while differing from each other, are faunistically much more like each other than the mainland.

3. The fauna is in many ways strikingly depauperate; many groups of animals which are common even in Central America are absent on the islands.

4. There is a multiplication of species and even sometimes of genera in some groups on the islands through radiative evolution and setting off of localized forms.

Part I of No. 2—Darlington

In the course of this report I shall seek to establish that these statements are true as concerns the Sphingidae of our region. The three tables I, II and III, if consulted with these four statements

[7] Mayr, Ernst, 1946, History of N. American Bird Fauna, Wilson Bull., vol. 58, pp. 3-41.

[8] Darlington, P. J., Jr., 1938, The Origin of Fauna of Greater Antilles, Quart. Rev. of Biol., vol. 13, pp. 274-300.

in mind, bear out this conclusion in a very satisfactory way. Darlington says further: "What the orderliness shows most clearly is that the present Greater Antillean fauna has accumulated through series of immigrations at a time when the conformation of the land was not so very different from what it is now. . . . there has been no wide-spread extinction of animals since the fauna originated. *It is just about inconceivable* [italics mine] that, if the present fauna were derived from a larger fauna of continental type by *extinction* [italics mine] of many forms, the remnants would be distributed in such an orderly way, along what appear to be original migration routes. I think it is safe to conclude, then, that the Greater Antillean fauna is an *accumulation* of immigrants, *not the residue of a larger fauna* [italics mine]. . . . the fauna as a whole does *not* divide into a group of older residual forms and a group of more recent immigrants. . . . There never was a time when free communication with either North or South America would have been expected to bring such a limited fauna to the Greater Antilles." (See Table IV.) An interesting example of the depauperate butterfly fauna of the Antilles as compared with the Island of Trinidad which is part of a continental shelf and has a rich continental fauna was given by Marston Bates[9] in his "Butterflies of Cuba" where he reports only 156 species of butterflies from Cuba as compared with 289 from Trinidad. There is a striking general occurrence of wide-ranging, strong-flying butterfly groups in the West Indies, and there is an absence for the most part of butterflies belonging to weak-flying, non-migratory groups.

However there is, in the Greater Antilles, one group of non-migratory, weak-flying butterflies called the Ithomiidae. These are the frail, transparent winged butterflies, one group of which is found in Cuba and one in Jamaica-Hispaniola. Dr. Richard Fox who has worked over this group, published in 1949 "The Evolution and Systematics of the Ithomiidae".[10] He states his

[9] Bates, Marston, 1935, Bull. Mus. Comp. Zool. vol. LXXVIII, no. 2, pp. 65-258.

[10] Fox, Richard, 1949, pp. 1-12. Preprint of an abstract of a Doctor's Dissertation, Univ. of Pittsburgh Bull., vol. 45, no. 8, June 5, 1949. Title of dissertation when published will be, "Some Historical Factors in the Present Distribution of the Ithomiinae in Tropical America."

belief that the two species of ithomines in the West Indies reached the islands when they were part of the Central American mainland—Eocene or Oligocene. He also believes that the places where they are now found were never under water at any time during the Tertiary. Thus for their distribution we must presuppose the Honduras-Jamaica connection or at least a very narrow stretch of water between them. In a letter to me Dr. Fox states that the ithomines live in high rain forests and it is most difficult to believe that they were rafted to the Antilles or blown there in hurricanes. He says of them: "They don't fly anywhere, they can't survive salt water; they live in such a manner that hurricanes would need to uproot whole forests to transplant them. The weight of evidence suggests that they travel exclusively by land and probably not very rapidly, ... that is only through gradual expansion of range over thousands of generations." The distinguished Orthopterist, James Rehn, in talking this over with me says there is some evidence of sub-specific distribution among certain cockroaches from northern South America up through the Lesser Antilles to the Greater Antilles, except Cuba, where a Central American sub-species exists. Also there is a South American cockroach genus (flightless) which has gone as far as Puerto Rico. These insects, he feels with Fox, could not drift, blow, or fly and live in mountain forests as they do. We are in this paper dealing with Sphingidae, a group very late to evolve, and Marston Bates in his "Butterflies of Cuba" throws light on this contradiction on page 82[9] where he says that as far as butterflies are concerned, there may be all the land connections the most ardent believer in Land Bridges presupposes in pre-Miocene time, because there was in the Miocene in the West Indies a general submergence of all but the mountain tops. Enough things survived of older orders and older fauna to repopulate the islands, and that after this the nucleus of very old types in the West Indies has been supplemented by arrival since the Miocene. This would explain the frail, non-migratory ithomines and the flightless cockroaches as the ancient types, and we realize that we are looking at different geologic levels, no one of which tells the whole story.

Again Mr. Rehn pointed out that while fossil records do not show any widespread extinction of an ancient fauna in the Antilles, there is evidence of the extinction of certain large rodents in both Puerto Rico and Hispaniola. Some of these fossils are in rocks as late as Pleistocene and Pliocene. I quote these exceptions because I wish to be entirely accurate, although I believe, after the most careful study of the Sphingidae that these strong flying moths were borne to the Antilles either over water or through the air.

Islands of the Antilles Faunistically Alike, Resembling Each Other More Than the Mainland (Darlington, Point 2, Part 2)[11]

In the preceding paragraph we discussed part 1 of point 2 of Darlington's conclusions concerning the fauna of the Greater Antilles. We shall now discuss the second statement in point 2—that the Greater Antilles resemble each other faunistically much more than they resemble the mainlands, even Central America, whence without much doubt most of these island Sphingidae originated. Since the fauna of the Lesser Antilles as far as Sphingidae are concerned is so similar in most respects to that of the Greater Antilles, I shall in this and the next paragraph refer merely to the Antilles. I have shown in Table I the great similarity in genera and species in Mexico, Central America and South America. If we examine the endemics of the Antilles as shown in Table III we shall see a striking resemblance among the Antilles as to genera, and while the subspecies of the continental parent species differ on almost every island, owing to isolation and resulting geographic speciation, they nevertheless bear a far greater resemblance to each other than to the mainland Sphingidae. To illustrate, *Cocytius vitrinus* occurs in Cuba and Haiti and *Cocytius vitrinus musgravi* occurs in Jamaica. This species does not occur on the mainland. *Nannoparce poeyi* is found in Cuba, Jamaica and Haiti, not on the mainland. *Cautethia noctuiformis* occurs in Cuba, Haiti, Puerto Rico and the Lesser Antilles, and, although the genus is represented on the mainlands by two

[11] Darlington, P. J., Jr., Origin of Fauna of Greater Antilles, etc., Quarterly Rev. of Biology, vol. 13, pp. 274-300.

other species, *noctuiformis* is found only on the West Indies. *Xylophanes irrorata* occurs on Cuba, Haiti, and the Bahamas, but nowhere else. A few similar species of *Phlegethontius*, *Protambulyx*, *Amplypterus*, *Erinnyis*, *Hemeroplanes*, *Perigonia*, *Pholus*, and *Xylophanes* are found on the islands, while the mainland is rich in species of all these genera. There is, however, one most interesting contradiction in the sphingid fauna of the Antilles. The genus *Sphinx*, so unusually richly represented in Mexico has on the island of Dominica the sole representative of this genus among all the Antilles, *Sphinx tricolor*. How this *Sphinx tricolor* got to Dominica poses an interesting question; but we remember that Schuchert [12] said that the fauna of the volcanic Caribbees or Lesser Antilles as compared with the fauna of the limestone Caribbees resembled that of the mainland in general rather than that of the Greater Antilles. Certainly we must admit that unless recently introduced by some flotsam or by a ship, this lone example among Sphingidae bears out Schuchert's statement and is an exception to the heading of this paragraph.

Fauna of the Antilles Depauperate (Darlington, Point No. 3)

Darlington's [13] third conclusion on the distribution of the fauna of the Greater Antilles is: "The fauna is in many ways depauperate; many groups of animals which are common even in Central America are absent on the Islands." Figures, while not in this case 100 per cent accurate, certainly tend to prove this true for the Sphingidae of the Antilles at first sight—73 species on the Antilles (25 of which are strong flyers and are probably coming to the Islands from time to time now), 154 species in Mexico and Central America, and 223 in South America. To be more specific, there are four species of *Phlegethontius* on the Antilles, 20 in Mexico and Central America, 25 in South America. Of *Protambulyx* there are 2 on the Antilles; 3 in Mexico and Central America; 8 in South America. Of *Sphinx*, 1 is in the Antilles, 12 are in Mexico and Central America and 4 are in South

[12] Schuchert, Historical Geology of Antillean-Caribbean Region, pp. 102, 108, 754 ff.

[13] Darlington, P. J., Jr., Origin of Fauna of Greater Antilles, etc., Quart. Rev. of Biology, vol. 13, pp. 274-300.

America. Of the genus *Nyseryx* there are none in the Antilles, 5 in Mexico and Central America, and 16 in South America. Of *Pholus* there are 5 species and 4 subspecies in the Antilles, 8 species in Mexico and Central America and 18 in South America. The genus *Xylophanes* is represented on the Antilles by 10 species, 30 in Mexico and Central America and 53 on the South American continent. Table IV shows this accurately by genera and species. Now the flora of the Antilles is very rich and the food plants of many species of Sphingidae not found on the islands are found on the Antilles—food plants of sphingids abundant on the mainland. Certainly it seems unlikely to the writer who has had field experience on the Islands and in Venezuela and Guatemala, that these mainland species once lived in the Antilles and that their present fauna is relict or residual. The climate and food plants of the Antilles favoring the abundant mainland Sphingidae, why are they absent from the Antilles? Why are there so few of the species of such strong-flying genera as *Phlegethontius, Amplypterus, Sphinx* and *Pholus* on the Antilles? The depauperate Sphingidae fauna of the Antilles seems clearly to point to islands of oceanic origin, to distribution over water and through air rather than by land bridges or to islands which are continental fragments.

Speciation through Radiative Evolution as Illustrated by the Sphingidae of the Antilles (Darlington, Point No. 4)

In discussing Point No. 4 of Darlington,[14] he says: " Many of the groups which are best represented are characteristic of oceanic islands; and there has been a good deal of radiative evolution in the most significant groups," such as fresh-water fish[15] which after attaining the islands obviously underwent radiative evolution, thus increasing not only the number of species but also forming new genera. " Radiative evolution " is a term most often used by paleontologists, because, in their study of fossils, they are looking at the end results, and when we say that radiative evolution is evidenced in the Antilles we mean by that, that here

[14] Darlington, *loc. cit.*, pp. 274-300.

[15] In 1937 George S. Myers published in the Gen. Appendix to Smithsonian Report, pp. 339-364 (3 plates), an article called Fresh Water Fish and West Indian Zoography, and in it he points out that there are no truly Fresh Water Fish in the West Indies.

we find wholly new species existing side by side with widely distributed continental species, but this wholly new species is restricted to the Antilles. We also find wholly new genera among the Sphingidae. Radiative evolution has taken place over very long periods of time, geologically speaking, and is due to long geographic isolation. We might say then, that radiative evolution is the end result of geographic isolation of all kinds, whether by desert, high mountains, or insularity. Radiative evolution is of course going on all the time and as such is by no means an "end result" but a continuing process. We speak of it as an "end result" only as we view the new species, or genera. Although speciation through radiative evolution is by no means the most evident evolutionary process among Sphingidae of the Antilles, nor is it of primary importance in any consideration of the distribution of Sphingidae in the Antillean-Caribbean region, its evidence exists and is of great interest. As I have said before, but feel it important to repeat in this section of my report, the Sphingidae being strong fliers could most certainly have reached the Antilles over water by flight, on jetsam and flotsam and through the air via hurricanes. In the United States we tend to think of these hurricanes as originating in the Caribbean and blowing towards the mainland; but the history of great hurricanes shows that some have originated in the Central American and Gulf of Mexico regions and blown towards the West Indies, while others have changed their course and blown back towards the islands. However they originally arrived, however they continue to arrive, there is evidence in the origin of new species and even genera of radiative evolution among the Antillean Sphingidae.

In Jamaica we have the common Sphinx moth, *Epistor lugubris,* which occurs in Venezuela, Trinidad, Mexico, Central America, Florida and the Antilles. In Jamaica, however, flying in exactly the same localities and captured on the same nights at lights or over flowers in the Hope Gardens near Kingston, Jamaica, are *Epistor lugubris* and *Epistor latipennis,* the latter at first glance looking similar to *lugubris.* There is absolutely no record of hybridization or any evidence of it in a long series of these two moths run in parallel. B. Preston Clark[16] in his description of *latipennis,* says the following:

[16] Clark, B. Preston, 1920, Proc. New Eng. Zool. Club, vol. vii, p. 78.

"*Epistor lugubris latipennis,* R. & J., has been considered as the Jamaican subspecies of *E. lugubris lugubris,* Linne. At Mandeville, Jamaica, during December, 1919, and January, 1920, Mr. F. E. Watson took both the broad- and narrow-winged form. Examination of the genitalia shows the tooth of the left clasper to be shorter in this form. On the fore wing R2 is more projected. The two forms occur in one locality. It seems therefore proper to consider the Jamaican form as a distinct species, to be called *Epistor latipennis* (R. & J.)."

I have caught the two species at Hope Gardens in March, 1947, and in June, 1948.

Another illustration of radiative evolution on the Islands is to be found in *Erinnyis obscura.* This is a very variable species and there will be described later the many subspecies of this insect occurring in the whole Antillean-Caribbean region. However, in Cuba there are existing side by side *Erinnyis obscura obscura* Fabr., and *Erinnyis pallida* Grote. For a long time *pallida* was considered a subspecies of *obscura* but has now been granted specific status. On Jamaica a new genus has arisen—*Himantoides. Himantoides undata* Wkr., is a beautiful little moth resembling closely the genus *Cautethia,* but having longer antennae, and a peculiar, laterally compressed scaling of the posterior tibiae and of the first tarsal joint, lacking in *Cautethia. Cautethia noctuiformis* Wkr., is curiously enough found in Cuba, Haiti, Puerto Rico and St. Thomas, but never so far found in Jamaica. Has this unique genus *Himantoides,* then, developed through radiative evolution in geologic ages from the genus *Cautethia* or vice-versa? This we shall probably never determine, but this new genus and these two new species of *Epistor* and *Erinnyis* illustrate radiative evolution in the Sphingidae of the Antilles.

Radiative Evolution Among Sphingidae of Florida, Mexico, Venezuela

Leaving the Antilles for awhile, we find a good example of radiative evolution in Florida in the occurrence, side by side there, taken in the same locality the same night, of *Lapara coniferarum* and *Lapara halicarniae.* The latter species has been taken by us in the Okefinokee Swamp in southern Georgia, in Miami and

Florida City, Florida, the former in all these localities, too. Another example of a new species in Florida, occurring elsewhere only in the Bahamas, is *Protambulyx carteri*. We have caught *carteri* over night blooming Jasmine in Everglades City, and it is taken in Miami and Florida City. It seems largely to have replaced *Protambulyx strigilis* in Florida though there is a record of *strigilis* having been caught in 1919 on Chokoloskee Island on the west coast of Florida. *Madoryx pseudothyreus* is found only in Florida and Cuba, possibly blown to Cuba in some hurricane. It is certainly more abundant in Florida than in Cuba, according to all known records. Once my nephew and I caught in one week in Everglades City over Petunias at dusk 45 specimens of *Madoryx pseudothyreus* and we again caught three specimens there fifteen years later. No such abundant record exists for Cuba. *Isoparce cupressi* is a genus and species endemic to Florida and southern Georgia.

In Mexico we have several genera existing only there, namely, *Dolbogene*, *Trogolegnum*, *Monarda*, and *Gurelca*. *Phlegethontius kuschei* and *P. aztecus*, *P. barnesi* and *P. holcombi*; *Ceratomia igualana*, and *C. hoffmanni*; *Sphinx balsae* and *S. chisoya*, *Amplyperus globifer*, *Gurelca muelleri* and *G. sonorensis*; *Xylophanes hannemanni*, *X. muelleri* and *X. katharinae* are among the species found only in Mexico. All of these, being either genera or genuine species found nowhere else so far as recorded, would seem to be illustrative of radiative evolution, while in Venezuela we have *Phlegethontius franciscae*, *Protambulyx sulphurea* and *Orecta fruhstorfi*. Here so far we have found no new genus, and because of its position in a great continent, freely accessible from many directions, Venezuela is much more illustrative of geographical distribution by infiltration than origin of species through radiative evolution.

Formation of Subspecies on the Antilles as a Further Evidence of the Influence of Geographic Isolation on Speciation

Ernst Mayr[17] says, in "Systematics and Origin of Species": ". . . . geographic speciation is characterized by the gradual building up of biological isolating mechanisms during geographic

[17] Mayr, Ernst, 1942, pp. 187, 155, 180.

isolation. The primary factor is thus geographic segregation and isolation, and the secondary factor is the gradual accumulation of genetic differences leading to morphological, physiological, ecological, and ethological differences." The type of continuing evolution now in process on the islands, and most clearly marked in the whole region of this study, also, as far as Sphingidae are concerned, is called geographic speciation or the origin of new subspecies through isolation and geographic barriers of many kinds. Through geographic isolation certain Sphingid moths represented on the continent have produced on the islands subspecies. This tendency is widespread on both the Greater and Lesser Antilles with many endemics resulting. While most of these are classified as subspecies of the specific continental representative, if the parent species found continentally were introduced to the islands now, there might still be no natural interbreeding, and this would indicate that these subspecies had obtained specific rank.

Mayr says (*loc. cit.*, p. 155) : " A new species develops if a population which has become geographically isolated from its parental species acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down."

He goes on to say (*loc. cit.*, p. 180) : " The perfect demonstration of speciation is presented by the situation in which a chain of intergrading subspecies forms a loop or overlapping circle of which the terminal forms no longer interbreed, even though they coexist in the same localities."

Dr. W. T. M. Forbes [18] has made an interesting study of this kind of terminal overlapping in *Junonia lavinia*, a very common butterfly with innumerable subspecies both in the Antillean-Caribbean region and continentally wherever it is found. This butterfly colonized the West Indies from both South and North America. The two colonizing lines met in Cuba where they now live side by side without interbreeding.

In geographic isolation such as occurs on oceanic islands or where there are impassable mountains or deserts on continents

[18] Forbes, Dr. W. T. M., Variation in *Junonia lavinia* (Lep. Nymphalidae), Jr. N. Y. Ent. Soc., vol. 36, p. 306, 1928.

we find many instances among the Sphingidae of endemic subspecies brought about by geographic isolation. Table III shows the large number of these in the Greater and Lesser Antilles. In Jamaica, which is perhaps the island in our study longest of oceanic insular character, we have, to mention only a few, *Phlegethontius sexta jamaicensis*, *Amplypterus gannascus jamaicensis*, *Isognathus rimosa jamaicensis*, *Erinnyis obscura jamaicensis*, *E. domingonis pallescens*, *Pachylia syces insularis*, *Sesia tantalus eumelus*, and *Pholus vitis hesperidum*. In Cuba we have *Phlegethontius rustica cubensis*, *P. brontes cubensis*, *Amplypterus gannascus cubensis*, *Isognathus rimosa woodii*, *I. r. congratulans*, *Pachylia syces cubensis*, *Sesia titan cubensis*, *Pholus satellitia posticata* and *P. s. cinnamomea*, and *Xylophanes chiron cubanus*. Among the Lesser Antilles we have *Phlegethontius sexta lucia*, *P. afflicta bahamensis*, *P. rustica dominicana*, *Sphinx tri-color*, *Perigonia lusca major*, *Pholus vitis fuscatus*, *Xylophanes chiron lucianus*. There are many more but these will serve as examples. From Mexico and Central America we have a few endemic subspecies such as *Amplypterus gannascus fulvescens* and *A. g. interrupta*, *A. donysa dariensis*, *Erinnyis obscura socorrensis*, *Hemeroplanes pan denticulata*, *Arctonotus terlooi mooseri*. Venezuela, being continental, has few endemic subspecies among which we mention *Xylophanes germen yurakano*, though in the Carnegie Museum there was certainly a similar looking specimen from Peru. Trinidad boasts, so far, of one endemic subspecies—*Xylophanes neoptolemus trinitas*.

Certainly some species seem much more frequently than others to give rise to geographic or regional subspecies, while other species even on oceanic islands remain very constant. Many of these constant forms are strong fliers, are adaptable as to food plant, and doubtless have made several immigrations into the Antillean-Caribbean region, from continental areas. *Pachylia ficus*, although it has different color variations occurring in the same locality (*aterrima*), is a constant species, as are *Pholus labruscae* and *Pholus fasciatus*. *Erinnyis ello* and *alope* remain constant, as do *Xylophanes tersa* and *pluto*, and many others. Of those in the region under study, which seem especially influenced by geographic isolation and especially illustrative of the origin of species through

geographic speciation, I shall illustrate with two—*Erinnyis obscura obscura* Fabr., and *Isognathus rimosa rimosa* Grote.

It is true that we are faced with genuine perplexity when it comes to differentiating between species and subspecies, but Ernst Mayr helps here again. In his book,[19] "Systematics and Origin of Species," he says: "Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups," and again, ". . . . how can we determine which of these isolated forms are 'potentially capable of inter-breeding'? Unfortunately there is no way of testing this in most cases, and we may as well admit that a decision is then possible only by inference."

Sometimes two species of the same genus overlap in range and there is a limited amount of hybridization without breaking down of the species limits. Dr. Walter Sweadner[20] in 1937 published his record of experiments with the genus *Platysamia* (saturnid moths). This report was called "Hybridization and Phylogeny of the Genus Platysamia." He found a limited amount of hybridization in nature where the range of *Platysamia cecropia* overlaps the range of the closely related species of *P. nokomis, P. columbia,* and *P. gloveri.* If no overlap existed and we had to classify these forms merely on the basis of their morphological distinctness, we would probably decide in most cases that they were subspecies. We all like to be very definite and make positive assertions as to species, subspecies, varieties, etc., but Dr. Sweadner's careful and remarkably painstaking and accurate work with the genus *Platysamia* points to the necessity for very great care in these classifications. He says, in part, in his conclusions:

"1. The genus *Platysamia* as analyzed here is an excellent example to illustrate the futility of attempting to set up rigid universal criteria for defining the limits of species or other taxonomic concepts even for such relatively homogeneous groups as the Lepidoptera.

"2. Intergrades can and do arise in nature through the process of hybridization.

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[19] Mayr, Ernst, Systematics and Origin of Species, 1942, pp. 120 and 166.

[20] Sweadner, Walter R., Hybridization and Phylogeny of the Genus Platysamia, 1937, pp. 224 and 225. Annals, Carnegie Museum, vol. XXV, pp. 163-242, 1937.

"3. Intergradation through hybridization is not necessarily the same as the hybridization that occurs during and after the differentiation of one subspecies from another, because, as in the case presented, there may not be complete fertility between the parent stocks.

"4. Without a knowledge of the geologic history of the forms studied, it would be difficult, if not impossible, to distinguish between hybrid intergradation and the transition stages between geographical subspecies, for these transition stages necessarily involve hybridization." ff.

Illustration from Sphingidae of the Influence on Geographic Isolation in Speciation

Erinnyis obscura obscura Fabr.

This is a small and most variable species in which the sexes are different, the male having a darker thorax than the female and a dark longitudinal band through the gray forewing and an oblique sub-anal streak. Both sexes have a gray fore and a reddish hind wing. The base of the hind wing has a gray border. The female has no streaks on the forewing but both sexes have two dark spots on the costal border of the forewing. This moth has a wide range over the whole tropical and sub-tropical regions of the Americas, occasionally going as far north as Canada. It is common in the West Indies and Trinidad.

Erinnyis obscura rhaebus Bsd.

This has a brownish thorax and brown markings and patches on forewing. This is from Cuba and Haiti, and has been recorded on the continent.

Erinnyis obscura stheno Hbn.

Forewing much shorter, the dark longitudinal band of male is sharply interrupted in the center and the apical part is connected with the sub-anal streak, forming a submarginal band. Genital apparatus slightly varied. Barbados and Lesser Antilles.

Erinnyis obscura jamaicensis Clark

This is very pale on thorax and forewing of both sexes and the longitudinal streak of the forewing of the male is feebly marked and oblique streak before hinder angle is absent. Brown spots on costal margin less distinct. Jamaica.

Erinnyis obscura conformis R. & J.

This is a small form, the male without the dark longitudinal streak and both sexes have gray thorax, marginal band of hind wing darker, the row of dots before it very intense. Galapagos.

Erinnyis obscura socorrensis Clark

This is still smaller and monotonously gray in color, the longitudinal stripe of the male marked only by a line. Marginal band of hind wing above very narrow, the row of dots indistinct. Revella Gigedo Islands on west coast of Mexico.

Erinnyis pallida Grote

This is a square-appearing moth with broader wings than *obscura,* is plain gray with only traces of the longitudinal line in the male. The hind wings are almost white with a reddish tinge near the body. It is a sturdier insect than *obscura,* although it was long considered a sub-species of *obscura* like the afore-noted sub-species. It is found in Cuba.

Where the typical or continental *Erinnyis obscura* occurs with a sub-species or with an evidently derived species such as *pallida* in Cuba and *obscura jamaicensis* in Jamaica (sub-species), the probable explanation is a double invasion—the first definitely older and having isolated stocks which evolved independently and a second invasion which has not absorbed the local forms already on their way to, or having achieved, specific status.

Isognathus is a genus closely related to *Erinnyis* and its species *Isognathus rimosa rimosa* Grote has the longest series of sub-species of any moth in our region. There are many varieties and sub-species of *Amplypterus gannascus* but many of these are mere differences in size and color, whereas sub-species of *rimosa* are definitely sub-species, some probably on the way to species status. Geographical speciation is evidently and graphically at work here.

Isognathus rimosa rimosa Grote

Forewing and thorax chalky grayish white, abdomen with distinct bands. Forewing with large white marginal spots. The black basal spot of forewing is absent or very small, the female without the longitudinal streak on forewing. Hindwing light yellow with a heavy black band reaching almost to the cell, with a lighter gray place at anal angle which is crossed with fine lines. Cuba, Haiti, Puerto Rico.

Isognathus rimosa inclitus Edw.

Collar striped brown, forewing more intensely marked blackish brown, and female is even more dusted with black, especially at inner margin of forewing. Marginal band of hind wing is narrower. Very large moth for *Isognathus* species, and very mottled in appearance. Black markings on forewing make a half circle. Mexico, Yucatan, Central America and Panama.

Isognathus rimosa papayae Boisd.

Smaller and generally lighter, more pepper and salt appearance. There are two stripes on forewing, lower one curving but not forming half circle. A white spot on forewing near thorax and a short black line extends from this. Marginal band of hind wing narrower. Light spot at anal angle striped with fine lines. Venezuela; Guiana; (Trinidad?).

Isognathus rimosa braziliensis Clark

Very close to *papayae* but forewing is more uniformly gray and less strongly marked. The ground tone is not white. The second discal line on underside of hind wing is less prominent than in *papayae* and there are traces of first discal line. Bands on abdomen less sharp. Brazil (São Paulo and Rio de Janeiro).

Isognathus rimosa occidentalis Clark

Intermediate between *papayae* and *braziliensis*. Large and bold half circle of black lines on forewing, here. Hind wing light yellow with broad monotonously dark band. Amazons.

Isognathus rimosa molitor R. & J.

Black band on hind wing very broad, reducing yellow area. Forewing very light gray. There are two rows of black spots on the outer edge of forewing but these are less regular than in *wolcotti*. Anal spot on hind wing has fine lines across it. Haiti.

Isognathus rimosa wolcotti Clark

This form from Puerto Rico seems to be a kind of connecting link between the Cuban *rimosa rimosa*, the Haitian *rimosa molitor*, the Jamaican *rimosa jamaicensis* and the continental form *rimosa papayae*. It shows points of resemblance to all of them. Banded abdomen. Large and light gray forewing shading to brown, like *jamaicensis* and *rimosa rimosa*, marginal band of hind wing is almost as narrow as that of *papayae*. The broad, light-gray outer marginal band on underside of both fore and hind wing is very

prominent. There are two even rows of black spots on outer margin of forewing. The two dark streaks on forewing are straight and have no tendency to curve and make the half circle. Puerto Rico.

Isognathus rimosa congratulans Grote and Robinson

Dr. Jordan of Tring is inclined to think that both *congratulans* and *woodii* are merely forms of *rimosa rimosa* from Cuba, but they are so very constant and so very striking that I am at least temporarily according them subspecies status. This is a very dark form with the marginal band very broad, almost to cell. The lower of the two black lines on the forewing is slightly curved downward. Cuba.

Isognathus rimosa woodii Ramsden

This is a most lovely moth. It has the effect of smoky blackness mixed with gray, and seems ghostlike. I think it is the handsomest of the rimosas. Smoky black all over except for narrow patch of yellow near body on hind wing, and a median whitish band on forewing, which is wider on costal margin, whence it extends to lower edge of forewing. Cuba.

Isognathus rimosa jamaicensis R. & J.

The border of hind wing is really gray, rather than black, and there are no lines in the anal spot. The two rows of black spots on outer edge of forewing, which are so clear in *wolcotti* and less clear in *molitor,* are here short black lines. Jamaica.

All of these subspecies have been carefully arranged in the magnificent Sphingidae collection at the Carnegie Museum, Pittsburgh, which is a combination of the collections of Oberthur, Holland, and Clark. Some of the material is scanty and some of these subspecies have been described from one or two specimens. This does not necessarily mean that these forms are very scarce, but indicates, rather, that much of the Antillean-Caribbean region has not been fully worked over. It would, however, take years of residence in each one of the islands for complete records. The Cuban Sphingidae have been much more thoroughly done than those of any of the other islands because of the residence, in Santiago de Cuba, of Dr. Charles Ramsden, an authority on Sphingidae, with an unexcelled collection of Cuban material. In Venezuela we shall soon have a complete check list because René Lichy, of Caracas, is in process of compiling one. This is a very difficult

job because of the size of Venezuela and its widely differing faunal and geographic regions. The Venezuela check list is made somewhat more possible, however, because of the unique position of the Portachuela Pass in the Aragua National Park. This pass is situated between two high mountains, Pico Periquito on the west and Pico Guacamayo on the east. This pass is the watershed between the Caribbean and Lake Valencia and is situated in an undisturbed cloud forest which covers this part of the Coastal Range of the Andes. Up this pass, attracted at night by a 200 watt electric light bulb attached near the roof of Rancho Grande fifty feet above the road, fly myriads of all kinds of insects, so that one gets here, especially on nights of neblina or mountain fog, Sphingidae flying from the tropical lowlands of Ocumare and Turiamo, as well as many mountain forms. René Lichy has collected here and has done much collecting near the Rio Borburata and in the high Andes near Merida. In our collecting there in June, 1949, as well as in many years of collecting there by Lichy and the entomologists of Maracay, and for parts of three years by Dr. Beebe and Henry Fleming, new species for Venezuela are constantly being recorded. Lichy is finding a good many species which are drifting southward from Mexico and Central America. Besides my own collecting trips to Jamaica, I am receiving valuable assistance from C. Bernard Lewis, Director of the Institute of Jamaica, at Kingston, from Miss Lily Perkins, of Claremont, and Miss May Davis, of Mandeville, Jamaica. However, on a mountainous island like Jamaica, with some arid country, with an almost impassable rocky cockpit country and the high mountains of the Blue Mountain Range, there are undoubtedly many isolated pockets which will for years yield treasures to the student and collector—treasures perhaps quite unrecorded in science. All that any paper of this kind can hope to do is to give a general survey of known geographical regions and to draw conclusions from material in hand, knowing well that future work will add to knowledge and perhaps prove faulty the work of present students.

The Bearing of Work Done on the Galápagos Islands upon the Antillean-Caribbean Region

The foregoing paragraphs dealing with the evidence of radiative evolution of long-isolated species into other species or even into new genera, and with the far greater evidence on the Antilles of the continuing influence of geographic isolation in the origin of species in what is called geographic speciation, producing groups of isolated subspecies which may well be in process of developing into species, have been helpful in showing evolution at work in the Sphingidae of the Antillean-Caribbean region. Feeling, as I think the evidence shows, that the distribution of Sphingidae on the Antilles is largely due to dispersal by air or over water from Central America and some from North America, and that these islands are oceanic in origin as far as the distribution of Sphingidae is concerned, I think it will prove of great interest to study the evidence of the influence of geographic isolation in the evolution of the Sphingidae found on a clearly oceanic group of islands.

The Galápagos islands are situated 600 miles off the coast of Ecuador and have long been a magnet for scientific investigations and studies. Much that is mysterious and alluring has been written about these partly desert, wild and forbidding, isolated islands and there are valuable records of scientific expeditions. The California Academy of Sciences has been especially interested in the Galápagos and has worked with Julian Huxley and other British and American scientists. The Academy published, in 1945,[21] " The Galapagos Finches, a Study in Variation," by David Lack. Since many of his findings about the finches have bearing on the work done by Francis X. K. Williams under the Academy of Sciences of California, this work called [22] " A Study of the Butterflies and Hawkmoths of the Galápagos Islands," 1911, and of B. Preston Clark's later " Revision of the *Protoparces* [*Phlegethontius*] of the Galápagos Islands," [23] 1926, I shall quote several selections from Lack's careful study.

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[21] Lack, David, Occas. Pap. Calif. Acad. Sci., no. 21, pp. 117-118, 1945.

[22] Williams, Francis X. K., Proc. Calif. Acad. of Sci., vol. I, 4th Series, 1911.

[23] Clark, B. Preston, Proc. New Eng. Zool. Club, vol. IX, pp. 67-71, 1926.

In dealing with the whole subject of the evolution of island forms, Lack finds, for the different Galápagos islands, exactly what I have found for the islands of the Antilles and largely also for the other regions of this study, that there is no evidence in favor of the supposition that the differences between the island forms of each species are of adaptive significance. Like the different islands of the Galápagos, the islands of the West Indies have similar food plants and in the main a similar ecology. The parasites for the larvae of any one species appear to be about as abundant on one island as on another. This follows the theories of Sewell Wright and others, who, as Lack says, have demonstrated "on theoretical grounds that provided an isolated population is sufficiently small, it will after a time become different from a neighboring isolated population, although starting with the same gene complex, without the operation of natural selection, owing to the fact that the rate of gene elimination is quicker than the mutation rate. In each population it is partly a matter of chance which genes are eliminated, so that each population becomes stable at a different level. Given a sufficient length of time, such differences must arise provided the populations are small and isolated, and will arise irrespective of any difference between the environments of the populations." Hybridization seems in the finches to have played a rather small and unimportant part in the origin of species, but insufficient work has been done on the Galápagos Sphingidae to conclude that this is true also for them. To sum up the conclusions of Lack on the origin of species of the finches of the Galápagos Islands, we might say briefly that the observable facts seem to bear out the conclusion that it is the opportunities for isolation and subsequent re-meeting which have been primarily responsible for the evolution of the finches—not an exceptional variability. Hence we see that a primary requirement for species formation is geographic isolation with possibilities of re-meeting later. In the insects of oceanic islands, Buxton,[24] 1938, notes as we have already done with the Sphingidae of the Antilles (Table III) the high proportion of endemics. Here also, however, as far as Sphingidae are concerned, seems to exist an extreme tendency

[24] Buxton, P. A., 1938, The Formation of Species among Insects on Samoa and Other Oceanic Islands, Proc. Linne. Soc. London, 150th Session, pt. 4, pp. 264-267.

to variability in certain species such as *Erinnyis obscura* and *Isognathus rimosa*.

B. Preston Clark,[25] 1926, published "A Revision of the *Protoparce* (now called *Phlegethontius*) of the Galapagos Islands." Clark was not a field entomologist, did not rear species nor do active field collecting himself; but he was a careful and accurate taxonomist, had access to all the collections in America, and was in constant contact with Karl Jordan, of Tring, England. He believes that there has been so far only one specimen of *Phlegethontius calapagensis* and this one specimen is in the Holland collection in Carnegie Museum. He believes that this species was neither seen nor collected by Williams in 1905-1906. Of the other members of the *Phlegethontius* bred and collected by the expedition of the Academy of Sciences of California, Clark records *Phlegethontius rustica postscripta* as much the most common of this genus on the islands. This has a light and dark phase and feeds on a great variety of plants, eating *Cordia lutea*, a member of the Borage family, and *Clerodendron molle* (Verbena family). The parent, continental form, *Phlegethontius rustica*, feeds on the Verbena family. The subspecies *postscripta* was frequently parasitized as a larva, but was on the whole the most plentiful of the *Phlegethontius*, the moths being frequently caught at dusk over fragrant flowers. *Phlegethontius leucoptera*, which is a very light moth, was reared from larvae feeding on a low, succulent solanaceous plant found at Wreck Bay on Chatham Island, at Iguana Bay on Albermarle Island and at Tagus Cove. *Phlegethontius nigrita*, whose imago has white instead of yellow spots on abdomen and has body above and wings entirely brownish black, narrow pointed wings, white stigma and two rows of white spots dorsally on abdomen, has a larva which prefers *Eriger on* or *Croton*. The total list of all Sphingidae collected on the Galapagos are:

Herse cingulata Fabr., *Phlegethontius leucoptera* R. & J., *Phlegethontius rustica postscripta* Clark, *Phlegethontius nigrita* R. & J., *Phlegethontius calapagensis* Holland (not collected by Calif. Academy of Sciences 1905-6 but may still be there), *Erinnyis ello* Linne, *Erinnyis obscura conformis* R. & J., *Epistor lugubris* Linne, *Xylophanes tersa* Linne, *Celerio lineata* Fabr.

[25] Clark, B. Preston, 1926, Proc. New Eng. Zool. Club, vol. 9, pp. 67-71.

Of these, *Herse cingulata* is a widely distributed and strong flying insect, having been captured 300 miles out over the ocean. This moth has undoubtedly colonized from the continent and probably has made frequent migrations. Any member of *Convolvulus* suits its larva as a food plant. *Erinnyis ello*, *Pseudosphinx tetrio*, *Xylophanes tersa* and *Celerio lineata* are also widely distributed with larva feeding on food plants common everywhere. Although smaller than *cingulata*, both *ello* and *lugubris* are very strong fliers and wherever *tersa* and *lineata* are found they seem resistant to change. They may have been blown to the Galápagos by hurricanes, brought more recently by ships, or have been carried there on flotsam. *Erinnyis obscura obscura* has been there a long geologic time, since it is now subspecies *obscura conformis*. *Phlegethontius rustica postscripta* has its parent form *rustica rustica* on the continent, and *nigrita*, I think, has probably in the far distant past had the same parentage. It resembles *rustica rustica* in some of its wing patterns, although its wing shape is quite different from *rustica rustica* and this may invalidate *rustica rustica* as the parent species. One can see then, in the strictly oceanic islands, Sphingidae showing exactly the same type of geographic speciation as is occurring on the Antilles. It is greatly to be hoped that because of their unique flora and fauna, because of their geologic age and isolation, and because of their strictly oceanic origin, the Galápagos Islands may be set apart for all time as a refuge and a natural scientific laboratory. Before World War II this was being strongly advocated by groups of American and British scientists. There is here something which is unique, much of it still unspoiled by man and primeval in character and we should press for their preservation, having if possible eliminated those destructive introduced animals such as wild dogs, pigs, etc. These are fast destroying the endemic flora and fauna.

Hybridization Among the Sphingidae in the Regions of Our Study

There is on continental areas, where there is a wide variety of the species of the same genus, an interesting possibility of natural hybridization where two closely related species overlap in range. Dr. Walter Sweadner,[26] of the Carnegie Museum, has done a most

[26] Sweadner, Walter R., 1137, Hybridization and Phylogeny of the Genus *Platysamia*. Ann. Car. Mus., vol. XXV, pp. 163-242.

interesting piece of research on the hybridization of the moths in the genus *Platysamia*. I have already referred to his careful work when discussing the difficulty of drawing definite lines in all cases between species, subspecies, varieties, etc. There has also been much experimental work done with artificial hybridization among Sphingidae by British scientists. Sweadner's work in hybridizing the exceedingly similar species of the genus *Platysamia,* in observing the natural hybrids where the zones of two species overlap, and in successful hybridization artificially of these species with one another, was done across the breadth of our wide North American continent. The work was all done in the temperate zone where the temperature range of one zone is not as widely different from another as in a mountainous, tropical region. The species he worked with are relatively abundant as is to be expected in temperate climates where there are generally fewer species but much more numerous members of each species than in tropical or subtropical countries, where the number of species is numerically high and the individuals of each species relatively few. Although there are two ranges of mountains to be crossed from east to west in this country, one of which is high in places, the food plants of the larvae of the *Platysamia* are pretty generally distributed even in the high parts of their range. There are deserts and where these occur there was no overlap of range of two species, and no natural hybridization. It would be of great interest to follow Dr. Sweadner's work by observing possible overlap of range of the genus *Sphinx* among the North American Sphingidae, especially of *Sphinx vashti, Sphinx chersis* and *Sphinx perelegans.* But on mountainous, oceanic islands with their great diversity of habitat and climate, in tropics or sub-tropics, and in large countries like Mexico and Venezuela we find so many natural, impassable barriers that a study of natural hybridization would be almost impossible. Besides, hybridization would seem to play a small part in the process of speciation among the Sphingidae under study. Mayr [27] feels that hybridization plays a negative role in speciation: ". . . . hybridization was caused by the breaking down of an isolating mechanism, usually by the lifting of a geographic barrier.

[27] Mayr, Ernst, 1942, Systematics and Origin of Species, p. 270.

The result was that two populations or two subspecies, or two representative species, which up to that time had remained distinct and well separated units, began to mix and to eliminate the gap that had previously existed between them. Instead of furthering speciation, that is the establishment of discontinuities, hybridization has in all these cases, accomplished just the opposite."

Food Plants in Relation to Distribution of Sphingidae

Although sphinx moths, like birds, are equipped with wings and are strong flyers, although like birds, they seem to have been distributed on oceanic islands through the media of hurricanes, flotsam and jetsam, etc., where the distances over salt water were too great for flight, and although isolation through geographical or climatic barriers of many kinds accounts in large measure for the origin of new species and sub-species—in one very important respect the distribution of Sphingidae differs from that of birds or any type of winged mammal.[28] Sphingidae can reproduce and establish themselves only where food plants suited to their larvae exist. Hence a brief survey of food plants is necessary in any report on the distribution of Sphingidae.

We find upon consulting Table I that there are 23 species that fly in all five regions covered by this study, and two additional species that with slight variations, also occur in all five. These two species that occur with slight variations are *Pholus satellitia* and *Pholus vitis*. The food plants of these species, where known, are listed below:—

Herse cingulata Fab.

Food plants: *Ipomoea*, morning glory, sweet potato, etc. These plants are widely distributed in all regions under study and the eggs of this moth or even the larvae have probably been introduced wherever the sweet potato was not native.

Cocytius anteus Drury

Cocytius anteus medor Stoll.

Larvae of these moths feed on members of the Annona family where we find Custard apple and Paw-Paw. The special food

28 Among exceptions to this statement is the curious *Noctilio* genus of bats which feeds only on fish and we all know that among birds the Limpkins feed only on a certain variety of snail's eggs.

plant of *anteus* is *Annona cherimona.* The Annonaceae are very common in the tropics and we found many varieties in the Cloud Forest of Venezuela, on the leaves of one of which two young larvae of *medor* were feeding.

Cocytius duponchel Poey.

Larvae also feed on members of Annona family.

Phlegethontius sexta Johanss. (and subspecies)

Food plants: Solanaceae (Nightshade family), Jimson weed, tobacco, tomato, etc. Wherever tobacco and tomato are found this sphinx is common. Whether introduced to Venezuela with tobacco, or native there, it is difficult to say, since a wild variety of Nightshade is very common on the roadways there.

Phlegethontius rustica Fab. (and subspecies)

In the United States *rustica* feeds on members of the Bignonia family; but in the more tropical regions under study its food plants may be *Bignonia jasminifolia, Jasminum officinale, Duranta plumieri, Lippia citriodora* (verbena). *P. rustica* is a strong flying, easily adaptable moth, with some interesting subspecies in the Antilles.

Protambulyx strigilis Linn.

Food plants are members of the Anacardiaceae or Cashew family to which the Sumacs belong. Sometimes as in Small's Botany, Manual of Southeastern Flora, this family is called Spondiaceae and the Sumacs are called Spondias. The Cashew tree grows luxuriantly in both Jamaica and Venezuela.

Pseudosphinx tetrio Linn.

Feeds on members of the Apocynaceae family especially on a tree called Frangipani, (*Plumeria rubra, P. tenorii, P. obtusa,* etc.). This grows in many places in Jamaica and Venezuela. Several members of this family grow in Florida and of course the spreading Dogbane is very common in New England. *P. tetrio* certainly does not normally feed on Dogbanes but this moth is a straggler into southern New England and my nephew caught a beautiful, fresh specimen on a light pole in Brown's Mills, New Jersey. It may be blown north in southeast storms.

Erinnyis alope Drury.

Food plants: *Papaya carica* which grows in Florida and on Florida Keys, Allamanda which is a prickly shrub of the Florida

hammocks, of the Apocynaceae family. It also feeds on *Jatropha*, a *Euphorbia*. The papayas and euphorbias are all common in regions under this study.

Erinnyis ello Linn.

Larvae common on cassava, a member of the Euphorbias and on several other Euphorbias. It feeds on *Poinsettia*, *Yucca* and *Papaya*. It also feeds on *Cnidoscolus* or spurge-nettle found on hammocks and sand dunes of Florida.

Erinnyis oenothrus Stoll.

Feeds on members of the Apocynaceae family such as Oleanders.

Erinnyis crameri Schs.

Food plants: *Papaya* and *Allamanda*.

Erinnyis obscura Fab.

Feeds by preference on a creeping vine of the *Asclepias* family, called *Gonolobus*, a variety of which is found as far north as the Susquehanna River in Pennsylvania. The *Gonolobus* is not recorded from Jamaica, nor did we find it in Venezuela. There are several asclepias in both countries, however, but since the moths frequent the male *Papaya* trees in Jamaica in great numbers, it is likely that the larvae feed on this plant.

Pachylia ficus Linn.

Food plants are many varieties of *Ficus* including the common fig tree of orchards. Larvae occasionally found on leaves of *Cecropia* trees, the favorite food plant of *Pachylia syces*.

Pachylia resumens Wkr.

Larvae feed on members of the Apocynaceae family, especially *Echites echites* of the pinelands of Florida and the Florida Keys, a vigorous vine with opposite leaves, stems and branches intertwined and quite large flowers. This vine is often called Rubber vine or Devil's potato, and in Jamaica *Echites repens* is called White Nightshade and a closely allied plant called Yellow Nightshade.

Hemeroplanes parce Fab.

Food plant is probably some member of the Apocynaceae family but the larva has never been described. *Hemeroplanes inuus* does feed on *Ambelania tenuiflora* belonging to Apocynaceae family.

Epistor lugubris Linn.

Food plants: *Ampelopsis, Vitis, Cissus.*

Sesia tantallus Linn.

Food plant probably of Rubiaceae family since both *titan* and *fadus* feed on members of this family.

Sesia fadus Cram.

Food plant: *Genipa americana,* a member of Rubiaceae family.

Pholus satellitia Drury.

Food plants: *Vitis, Ampelopsis, Cissus.*

Pholus vitis Linn.

Food plants: *Vitis* and *Cissus.*

Pholus fasciatus Sulz.

Larvae feed on members of Onagraceae family where Evening Primrose and Willow-herbs belong. Its favorite food plant is *Jussiaea angustifolia* which occurs in swamps and low grounds of coastal plain of Florida and occurs also in many places in Jamaica where it is called Loosestrife.

Pholus labruscae Linn.

Food plants: *Eupatorium odoratum* and various *Vitis* and *Ampelopsis.*

Xylophanes pluto Fab.

This moth is frequently caught in the southern part of Florida and its food plant is given by Rev. Miles Moss, who reared it in Peru, as a member of the Erythroxylaceae family, the Coco or Cocaine producing shrub being a common member of this entirely tropical family. *Erythroxylon areolatum* is quite common in Jamaica. In southern Florida it probably feeds on *Chiococca alba* or *C. pinetorum,* both found here and on the Keys. This is a member of the Rubiaceae family.

Xylophanes tersa Linn.

Food plants: *Spermacoe,* herbs of the Rubiaceae or Madder family.

Celerio lineata Fab.

Food plants: *Oenothera, Portulaca, Epilobium, Vitis, Galium,* etc.

Now looking briefly at the food plants of these 25 moths found in all regions of this study, we shall I think, see, that while some of them are semi-tropical, most of these food plants are familiar

to the ordinary person, who is in no sense a botanist. The frangipani, *Ficus*, *Cecropia*, *Echites*, *Jussiaea* and *Erythroxylon* are semi-tropical but convolvulus, tobacco, nightshade, trumpet vine, verbena, custard apple, papaw, sumac, euphorbias, dogbanes, milkweeds, ampelopsis, grapevine, evening primroses and members of the Madder family are familiar to most of us. Hence the wide distribution of these 25 moths is due not only to strong flight but also to widely distributed and fairly common food plants.

A further study of the food plants of those moths found only in one or two localities, such as *Himantoides undata* of Jamaica and *Nannoparce poeyi* also of Jamaica, as well as of Cuba and Hispaniola, would throw further light on the relationship of food plants to distribution. These scarce or very local moths may in the case of *Himantoides undata* feed on members of the Rubiaceae family since the closely related species *Cautethia grotei* feeds on *Chiococca*. Occasionally, too, the larvae of moths seem to have adapted themselves to new food plants in isolated places. Sir Norman Lamont believes that in Trinidad, *Pholus vitis* has so adapted its habits because there are few grapevines in Trinidad.

The Sphingid Fauna of Mexico, Central America, Venezuela and Trinidad

Mexico is very rich in Sphingidae, having 145 described species. During glaciation in the Pleistocene many strictly North American species without doubt took refuge there and we find the following genera, all from the north:—*Sphinx, Ceratomia, Atreides, Smerinthus, Calasymbolus, Pachysphinx, Haemorrhagia, Ampelocca, Darapsa, Arctonotus, Proserpinus.* The genus *Pholus* has representatives in the temperate or nearctic zone, but it seems to be one of those intermediate groups about equally adapted to nearctic and neotropical climate. The genus *Dolba* is really indifferent, existing in Florida and also thriving in cold New England. *Epistor lugubris* and *Xylophanes tersa* are also wanderers in temperate North America but are much more identified with neotropical than nearctic climate. Certainly the greater number of Mexican species is tropical or sub-tropical, many having probably drifted into Mexico when the Isthmus of Tehauntepec arose, joining the two continents. There has, too, been some drifting south-

ward through Central America to Columbia. *Phlegethontius dilucida* was, until a few years ago, considered along with its close relative *Phlegethontius kuschei*, only from Mexico and Central America, but in 1942 Dr. Beebe and Henry Fleming caught it at Caripito, Venezuela, and later it was caught in the western part of Venezuela. *Phlegethontius corallina*, at one time thought confined to Mexico and Central America, has since been caught by René Lichy's friend Marc de Civrieux in the town of Valera in the western part of Venezuela. *Kloneus babyaga*, formerly only from Mexico and Central America, has been caught by René Lichy near the Rio Borburata in the Province of Carabobo, Venezuela. Another Mexican migrant which has apparently established itself in Venezuela is *Nyseryx tacito*. Three specimens have been caught in the valley of the Rio Borburata at an altitude of about 1900 feet. Probably as more thorough collecting is done in Venezuela and Columbia, more Mexican and Central American species will be found established there. Oswaldo Mooser, however, in his " Enumeracion de los Esfingidos Mexicanos," 1940,[29] gives the following list of Sphingidae so far known only from Mexico:

Phlegethontius kuschei Clark, *Phlegethontius leucophila* Gehlen, *Phlegethontius lefeburei bossardi* Gehlen, *Phlegethontius floristan cabnal* Schaus, *Phlegethontius floristan ishkal* Schaus, *Phlegethontius barnesi* Clark, *Phlegethontius crocala tepici* Clark, *Ceratomia igualana* Schaus, *Nannoparce balsae* Schaus, *Sphinx pseudostigmatica* Gehlen, *Sphinx adumbrata* Dyar, *Sphinx separatus melaena* R. & J., *Sphinx balsae* Schaus, *Sphinx chisoya* Schaus, *Amplypterus globifer* Dyar, *Trogolegnum pseudambulyx* Bsd., *Calasymbolus myops macrops* Gehlen, *Monarda oryx* Drc., *Erinnyis obscura socorrensis* Clark, *Hemeroplanes pan denticulata* Schaus, *Cautethia yucatana* Clark, *Nyceryx muelleri* Clark, *Ampeloeca myron mexicana* Gehlen, *Gurelca sonorensis* Clark, *Gurelca muelleri* Clark, *Arctonotus terlooi mooseri* Clark, *Xylophanes hannemanni* Clark, *Xylophanes muelleri* Clark, *Xylophanes katharinae* Clark.

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[29] Mooser, Oswaldo, 1939 (1940), Enumeración de los Esfingidos Mexicanos, Anales de la Escuela Nacional de Ciencias Biologicas, vol. I, pp. 407-495.

And to this list has been added since the above was done:

Sphinx pitzahuac Mooser, *Sphinx libocedrus achotla* Mooser, *Phlegethontius azteeus* Mooser, *Phlegethontius holcombi* Mooser *Ceratomia hoffmanni* Mooser.

The life zones of Venezuela are so varied they have almost limitless possibilities for habitat for living things. There is the Orinoco basin and the Llanos on its northern border. The Llanos are a vast grass-covered plain with scattered islands of woods. Dr. Beebe[30] has written a fascinating account of his trip to these Llanos. He says that they are accessible three times a year—in April, by car through a "horizon-wide dust bowl; in June, by muleback through fathomless mud and mire; in August, only a boat or amphibious truck can penetrate." There are wonderful lakes and small lagoons in April and to them come every animal living there—iguanas, tegus, jaguars, solitary, morose-tempered cimarrons or feral-bulls, thousands of ducks, herons and roseate spoonbills. The flora consists mainly of burned out stubble and far separated palms. Then there are the Guiana Highlands flanking the Orinoco, and these are often heavily forested. Much of the Orinoco Basin is submerged in the rainy season, but in some places there are wide, grassy plains. There is a branch of the eastern chain of the Andes, called the Sierra Nevada de Mérida, which proceeds northeastwards towards Trieste Gulf and the highest peak here is about 15,000 feet. Then there are the Coastal Andes which stretch east and west along the coast. These used to be heavily forested, but now except where protected they have been stripped and denuded and are deeply gullied, always brown except during the rainy season when a grassy stubble clothes them. There is the great Lake Maracaibo where lies the oil wealth of Venezuela, with the coastal highland on its eastern side and with lagoon-studded lowlands on the west. Further north is Puerto Cabello with the great unspoiled primeval forests of Rio Borburata where René Lichy has done extensive collecting. He says that the Coastal Andes with their numerous peaks over 6,000 feet are propitious for the spread of butterflies and moths from the high

[30] Beebe, William, Animal Kingdom, Bull. N. Y. Zool. Soc., vol. LII, no. 3, pp. 66-69, 1949.

Andes near Mérida. To prove this, he cites the following Sphingidae which he has captured there, moths known before only from the high mountains near Mérida: *Euryglottis aper, Stolidoptera tashasara, Epistor taedium australis, Xylophanes amadis meridanus,* and *Xylophanes pyrrhus.* Because of the Portachuela Pass near Rancho Grande, mentioned before in detail, we were able to capture some of these strays from the high Andes country ourselves in June 1949. *Euryglottis aper* is caught on a little higher Pass near Rancho Grande and we captured *Stolidoptera tashasara, Xylophanes amadis meridanus* and *Xylophanes pyrrhus* at Rancho Grande's high electric light. Dr. Beebe and Henry Fleming did much work at Caripito, which is in the northeast section of Venezuela, about a hundred miles from Trinidad. This gives a fairly clear, if brief, picture of the great variety of faunal zones in this mountainous land. There is for strong flying moths quite easy access from Colombia, Brazil and Guiana, and via Colombia from Central America and Mexico.

Trinidad is a rectangular chip of the Parian Shelf of Venezuela, raised into an island some fifteen million years ago. It is roughly about thirty by fifty miles or about the size of Rhode Island. Three high mountain peaks gave it the name of Trinidad. It has a famous pitch lake about 38 miles southeast of the capital, Port of Spain, and this is so famous a lake that we mostly think of it when we hear the word Trinidad. The soil of the island is very fertile and many tropical crops are grown successfully. There is at St. Augustine a well-known Imperial College of Tropical Agriculture about 7 miles from Port of Spain. It is equipped with free laboratories and experimental fields and is supported partly by the Imperial Government and by contributions from other West Indian Governments. From it has come much of the scientific knowledge of the flora and fauna of Trinidad. Rivers flowing down the mountainsides have formed charming valleys. Near the north central part is the Valley of Arima. In the center of this valley rises a sentinel hill and here has been found an ideal place to establish the permanent headquarters of the Department of Tropical Research of the New York Zoological Society, with Dr. William Beebe at its head. Here among high mountains, steep valleys and tropical forests is " Simla " once the home of a man

of wealth, but now the perfect spot for tropical research. Because of its continental origin as well as its nearness in miles to Venezuela (only 7 miles across the muddy Straits of the Dragon's Mouth), we find here a continental group of Sphingidae. These have been once listed by Kaye and Lamont,[31] in 1927, in a Catalog of the Trinidad Lepidoptera Heterocera (Moths), but little work has been done on them since and certainly many species that occur there are not listed. For instance, when I was working at the Carnegie Museum I found there quite a series of *Erinnyis obscura* from Trinidad, and this species is not mentioned in the catalog. Dr. Beebe and Henry Fleming, the entomologist of the Department of Tropical Research, are most careful observers and indefatigable recorders of data so that we hope that much that is new to science will be learned about Trinidad. Enough is known already to be quite sure that the Sphingidae migrated there from the nearby continent and that there are continuing migrations. Here we find little evidence of speciation due to geographic isolation or to oceanic origin, so important in the Antilles. *Xylophanes neoptolemus trinitas* is the only recorded subspecies endemic to the island, though perhaps others will be found because of the continuing work of Beebe and Fleming in this field. However, I definitely expect to find their work proving the existence of new species rather than endemics.

The Sphingid Fauna of South Florida

The southern end of Florida is the only sub-tropical section of this large state and it also is washed by the Atlantic as it merges with the Gulf of Mexico, so that we shall mainly discuss the Sphingidae found in the part of Florida south of Lake Okeechobee. This will give us the whole Everglades region, most of the Ten Thousand Islands, the Big Cypress, Royal Palm State Park, the Cape Sable region and the Florida Keys. Some of it including Royal Palm State Park, is now The Everglades National Park, a wild, well-watered area, much of it covered with a rich sub-tropical flora. It is also a region of hurricanes and certain moths quite common to this region, and probably endemic, have been blown or

[31] Kaye, Wm. James and Sir Norman Lamont, Mem. Dept. Agr., Trinidad and Tobago, no. 3, pp. 1-144, 1927.

carried in some way to the Bahamas and to Cuba. There has been infiltration from the north, but at least three of these infiltrations have Florida subspecies replacing the parent species of the north. These are: *Dolba hylaeus floridensis, Ampeloeca myron cnotus,* and *Amphion nessus floridensis.* Florida's greatest sphingid prize is a denizen of the cypress swamps and has crept up to the cypress of Okefinokee Swamp in Georgia, but at places only 4 miles from the Florida line. This moth is *Isoparce cupressi.* In our twelve visits to the Okefinokee Swamp we have never found either imago or larva of this rare moth, but our guides have seen the larva on the cypress trunks and one of them reported seeing many of the moths floating in the water near the cypress boles. These may have been dead of course. Florida shares *Phlegethontius brontes cubensis* with Cuba and we have caught it over flowers in Everglades City in early April. It also shares *Madoryx pseudothyreus* with Cuba. With the Bahamas, Florida shares *Protambulyx carteri* and *Cautethia grotei.* Again, with southern Georgia it shares *Lapara halicarniae.* We would not have known this, as there was no record from Georgia, had we not taken one freshly emerged, with still limp wings, in the Okefinokee Swamp. Table I shows how many sub-tropical Sphingidae Florida shares with the other regions of this study. When we realize that it has *Hemeroplanes parce* and *Perigonia lusca, Sesia titan, S. fadus,* and *S. tantalus, Xylophanes pluto* and *Epistor ocypete,* we know that Florida truly belongs, as far as Sphingidae are concerned, with these Caribbean countries, and in its more remote and untouched hinterlands, we, who have collected there, believe that much is still to be discovered. It is important, moreover, to state and re-state that recorded observations actually made in the field are in the end meager and that there is still much new to be learned of the sphingid fauna of the Antillean-Caribbean area. We draw our conclusions on what we have observed, leaving this interesting field wide open for future research.

Summary

1. Because of the presence on the Antilles of numerous endemics in the way of subspecies, species and even genera among the Sphingidae, these islands, as far as Sphingidae are concerned,

appear to be oceanic in origin rather than continental fragments.

2. This is further emphasized by the depauperate population of Sphingidae on the Antilles as compared with the very rich Sphingidae fauna of Mexico and Central America, from which the Antillean population of Sphingidae undoubtedly sprang. There is no evidence whatsoever that the present sphingid fauna of the Antilles is relict from a once richer fauna, or is residual.

3. We believe, therefore, that the Sphingidae have reached the Antilles from Central America and North America over water and through the air and that there have been and probably are continuing immigrations of strong flying species at various times. These immigrations account for the stability of these species on these islands and their exact similarity to the parent continental species.

4. Since there are 25 species that are common to all the regions of this study, it is of special interest to note that all of these have common and widely distributed food plants, and there seems a definite relation between food plants and distribution of Sphingidae.

5. In Mexico we believe that all evidence points to infiltration from the north and south.

6. Venezuela's large and varied continental population of Sphingidae is accounted for by infiltrations from Brazil, Colombia and Guiana as well as from Mexico and Central America through Colombia. These infiltrations are of course added to her original continental population of Sphingidae.

7. Trinidad, though an island, is really a fragment of the Parian shelf of South America and its fauna has come chiefly from Venezuela. There are continuing immigrations.

8. The Sphingid fauna of the Antilles is, as we have said, largely Central American and North American in character, but there has been a limited exchange from island to island, though the islands have been long separated.

9. The many natural barriers in Mexico such as deserts, high and dry plateau, high mountains, etc., have been favorable to the formation of endemic species and subspecies as has the isolation of the Antilles, whereas Florida, Venezuela and Trinidad are more continental in type, probably receiving new species through

infiltration, except where there is isolation because of natural barriers.

10. Speciation caused by geographic isolation is evidenced especially in Mexico and the Antilles.

11. There has been radiative evolution evidenced in the Antillean-Caribbean region in the appearance of new species and even new genera.

I hope that if you have followed this paper this far, something new has been added to the rather formidable word "Sphingidae." I dare to hope that these nectar-loving creatures are no longer just "bugs," but that because of their beauty and their aesthetic value as the chief fertilizing agent of the orchids, they have become worthy of observation. I hope they have grown to be for you, as they are for me, a part of the stillness, the mystery, the fragrance of the night. If so, they will bring to you a fresh understanding of the riddle of life upon the earth, and will help you to open your eyes, your minds, and your hearts to the wonders of this evolving world.

TABLE I. SPHINGIDAE OCCURRING IN AT LEAST 3 OF THE REGIONS UNDER STUDY

Florida	Jamaica	Mexico and Central America	Trinidad	Venezuela
Herse cingulata	*H. cingulata*	*H. cingulata*	*H. cingulata*	*H. cingulata*
Phlegethontius sexta	*P. sexta jamaicensis*	*P. sexta sexta*	*P. sexta paphus*	*P. sexta paphus*
Phlegethontius rustica in all five				
		P. albiplaga	*P. albiplaga*	*P. albiplaga*
		P. diffissa tropicalis	*P. difissa tropicalis*	*P. difissa tropicalis*
		P. hannibal	*P. hannibal*	*P. hannibal*
		P. lichenea	*P. lichenia*	*P. lichenia*
		P. floristan	*P. floristan*	*P. floristan*
		P. ochus	*P. ochus*	*P. ochus*
Cocytius anteus	*C. anteus* and *C. anteus medor*	*C. anteus medor*	*C. anteus medor*	*C. anteus medor*
Cocytius duponchel in all five except not reported from Trinidad, but probably there				
Protambulyx strigilis in all five				
	Amplypterus gannascus in all four			
Pseudosphinx tetrio in all five				
	Isognathus rimosa jamaicensis	*I. rimosa inclitus*		
		I. rimosa papayae		*I. rimosa papayae*
			I. scyron	*I. scyron*
Erinnyis ello in all five				
Erinnyis alope in all five				
Erinnyis obscura in all five				
Erinnyis domingonis	*E. domingonis pallescens*	*E. domingonis domingonis*		*E. domingonis domingonis*
Erinnyis crameri in all five				
Erinnyis oenotrus		*E. oenotrus*	*E. oenotrus*	*E. oenotrus*
Erinnyis lassauxi		*E. lassauxi* subsp.	*E. lassauxi* subsp.	*E. lassauxi* and a subsp.
Pachylia ficus in all five				
Pacylia resumens in all five				
	P. syces insularis	*P. syces syces*		*P. syces syces*
		Leucorhampha triptolemus	*L. triptolemus*	*L. triptolemus*

TABLE I (*Continued*)

Florida	Jamaica	Mexico and Central America	Trinidad	Venezuela
Madoryx pseudothyreus	*M. oiclus*	*M. oiclus* *M. bubastus butleri*	*M. oiclus* *M. bubastus bubastus*	*M. oiclus* *M. bubastus bubastus*
Hemeroplanes parce probably in all five, not reported yet from Trinidad				
Epistor lugubris in all five				
Epistor ocypete probably in all five but not yet reported from Trinidad				
Sesia fadus occurs in all five				
Sesia tantalus occurs in all five				
		S. ceculus	*S. ceculus*	*S. ceculus*
Pholus satellitia pandorus	*Pholus satellitia satellitia*	*P. satellitia lichaon*	*P. satellitia lichaon*	*P. satellitia lichaon*
Pholus vitis	*P. vitis hesperidum*	*P. vitis vitis*	*P. vitis vitis*	*P. vitis vitis*
Pholus fasciatus occurs in all five				
Pholus labruscae occurs in all five				
		P. anchemolus	*P. anchemolus*	*P. anchemolus*
		P. obliquus	*P. obliquus*	*P. obliquus*
Xylophanes pluto occurs in all five				
Xylophanes tersa occurs in all five				
	X. chiron chiron	*X. chiron nechus*	*X. chiron nechus*	*X. chiron nechus*
		X. tyndarus	*X. tyndarus*	*X. tyndarus*
		X. neoptolemus	*X. neoptolemus*	*X. neoptolemus*
		X. anubus	*X. anubus*	*X. anubus*
		X. thyelia	*X. thyelia*	*X. thyelia*
Celerio lineata occurs in all five				

Notes of Special Interest on Table I

1. The large, strong-flying Sphingidae such as *Herse congulata, Phlegethontius rustica, Cocytius anteus, Protambulyx strigilis, Erinnyis ello* and *E. alope, Pachylia ficus* and *P. resumens, Pholus satellitia* and *P. forma, Pholus vitis, P. fasciatus* and *Pholus labruscae* may have been dispersed by flying over great distances.

TABLE I (*Continued*)

Certain of these such as *Phlegethontius rustica (postscripta)*, *Erinnyis ello* and *Herse cingulata* are even found on the Galápagos Islands which are 600 miles from land.
Herse cingulata has been caught 300 miles out over the ocean.

2. Some of these moths have very common and widely spread food plants.
Herse cingulata will eat many kinds of *Convolvulus* and sweet potato.
Cocytius anteus will eat many of the Anonia family.
Phlegethontius sexta eats tobacco, tomato and Nightshade family in general.
Phlegethontius rustica eats many Bignonias (Trumpet vine family) and Jasmines.
Pseudosphinx tetrio eats species of Plumeria family.
Erinnyis alope eats Paw-paw, etc.
Erinnyis ello eats Euphorbias, Poincettias, etc.
Erinnyis obscura eats Asclepias and probably Paw-paw.
Pachylia ficus eats fig.
The Pholus family in general eat various members of the Vitis family.
Xylophanes tersa eats Spermacoe or buttonweeds.
Celerio lineata eats evening primrose, willow herb, etc.

3. Some have been introduced by man in introducing food plants commercially:—
Herse congulata on sweet potato.
Phlegethontius sexta on tobacco.
Erinnyis alope and *E. obscura* on Papayae.

4. Note the greater similarity of species in the more tropical countries of Trinidad, Venezuela, Mexico and Central America, as contrasted with Florida and Jamaica.

TABLE II. SPHINGIDAE ENDEMIC TO EACH OF FIVE COUNTRIES

Genus	Florida	Jamaica	Mexico and Central America	Trinidad	Venezuela
Cocytius		*C. vitrinus musgravi*			
Phlegethontius		*P. brontes brontes*	*P. aztecus*		*P. franciscae*
		P. sexta jamaicensis	*P. kuschei*		
			P. lucetius nubila (Costa Rica)		
			P. lefeburei bossardi		
			P. sesquiplex		
			P. muscosa		
			P. lanuginosa		
			P. barnesi		
			P. holcombi		
Dolba	*D. hylaeus floridensis*		*D. clarki*		
Dolbogene			*D. hartwegi*		
			D. manni		
Ceratomia			*C. hoffmanni*		
			C. igualana		
Isoparce	*I. cupressi*				
Nannoparce		*N. poeyi poeyi*	*N. poeyi haterius*		
Sphinx			*S. lugens*		
			S. geminus		
			S. biolleyi (Costa Rica)		
			S. pseudostigmatica		
			S. separatus melaenia		
			S. istar		
			S. praelongens		
			S. lanceolata		
			S. adumbrata		
			S. libocedrus achotla		
			S. balsae		

TABLE II (*Continued*)

Genus	Florida	Jamaica	Mexico and Central America	Trinidad	Venezuela
Lapara	*L. halicarinae*				
Protambulyx	*P. carteri*		*P. xanthus* (Costa Rica)		*P. sulphurea*
Amplypterus		*A. gannascus jamaicensis*	*A. gannascus fulvescens*		
			A. gannascus interrupta		
			A. globifer		
			A. donysa		
			A. donysa dariensis		
Orecta					*O. jahnstorferi*
Trogolegnum			*T. pseudambulyx*		
Monarda			*M. oryx*		
Isognathus		*I. rimosa jamaicensis*			
Erinnyis		*E. obscura jamaicensis*	*E. obscura socorrensis*		
			E. yucatana		
		E. domingonis pallescens			
Pachylia		*P. syces insularis*			
Madoryx	*M. pseudothyreus*				
Hemeroplanes			*H. pan denticulata*		
Epistor		*E. latipennis*			
Pachygonia			*P. drucei* (Panama)		
			P. ribbei		
Himantoides		*H. undata*			
Cautethia	*C. grotei*		*C. spuria*		
			C. yucatana		
Nyceryx			*N. eximia* (Panama)		
			N. mulleri		
Perigonia		*P. jamaicensis*			

TABLE II (*Continued*)

Genus	Florida	Jamaica	Mexico and Central America	Trinidad	Venezuela
Sesia		*S. blaini* *S. tantalus eumelas*			
Pholus		*P. satellitia* *P. vitis hesperidum*	*P. elisa*		*P. adamsi*
Ampeloeca	*A. myron cnotus*				
Gurelca			*G. muelleri* *G. sonorensis*		
Arctonotus			*A. terlooi mooseri*		
Amphion	*A. nessus floridensis*				
Xylophanes		*X. chiron* *X. jamaicensis*	*X. adalia* (Panama) *X. hannemanni* *X. juanita* *X. zucheri* (Costa Rica) *X. rhodina* (Panama) *X. godmani* (Panama) *X. acrus* (Panama) *X. belti* *X. muelleri* *X. turbata* *X. damocrita* *X. jordani* (Costa Rica)	*X. neoptolemus trinitas*	*X. germenyurakano*

Notes of Special Interest on Table II

1. By far the largest number of endemics are to be found in Mexico and Central America but we must remember that here we are comparing only one of the Antilles, the island of Jamaica, and when we look at Table III we shall see that the Antilles have many endemics.

TABLE II (*Continued*)

Second in number of endemics on this chart is Jamaica.

There are very few from Trinidad, which may be due to comparatively recent work on Sphingidae having been done there and also even more probably to its nearness to Venezuela (only 7 miles in one place) from which it has probably received and continues to receive most of its sphingid fauna.

Venezuela also has few endemics and this is probably due to the fact that it is continental and many forms have access from several directions.

2. Florida's endemics are especially interesting and follow Florida's division into warm temperate northern part and sub-tropical southern end, two being of southern origin, *Madoryx pseudothyreus* and *Protambulyx carteri*, while two, *Lapara halicarinae* and *Isoparce cupressi* she shares with Georgia to the north.
3. Mexican endemics seem readily attributable to northern infiltration of genus *Sphinx* breaking up through evolution into many new species, and to a larger tropical infiltration from Central and S. America.
4. The long extent of Mexico and Central America allows for great variation in climate and a wide difference in floral and faunal distribution. Also the great variety in physiography from tropical coastal regions to high plateaus and deserts and very high mountains makes for geographical isolation, favorable to endemics.

TABLE III. SPHINGIDAE ENDEMIC TO THE ANTILLES

Genus	Cuba	Jamaica	Hispaniola	Puerto Rico	Lesser Antilles
Cocytius	*C. vitrinus vitrinus*	*C. vitrinus musgravi*			
Phlegethontius		*P. sexta jamaicensis*			*P. sexta lucia*
					P. afflicta bahamensis
	P. rustica cubana		*P. rustica dominicana*		*P. rustica harteri*
	P. brontes cubensis	*P. brontes brontes*	*P. brontes haitiensis*	*P. brontes smythi*	
Sphinx					*S. tricolor*
Nannoparce	*N. poeyi*	*N. poeyi*	*N. poeyi*		
Protambulyx					
Amplypterus	*A. gannascus cubanis*	*A. gannascus jamaicensis*			*P. carteri* (Bahamas)
Isognathus	*I. rimosa rimosa*				
	I. rimosa congratulans	*I. rimosa jamaicensis*	*I. rimosa molitor*	*I. rimosa wolcotti*	
	I. rimosa woodii				
Erinnyis	*E. pallida*	*E. obscura jamaicensis*			
	E. guttularis	*E. domingonis pallescens*	*E. guttularis*		
Pachylia	*P. syces cubensis*	*P. syces insularis*			
Hemeroplanes	*H. ramsdeni*				
Epistor		*E. latipennis*			
Perigonia	*P. divisa*	*P. jamaicensis*			*P. thayeri*
	P. lefebrai		*P. lefebrai*		*P. lusca major*
			P. manni		*P. bahamensis*
Himantoides		*H. undata*			
Cautethia	*C. noctuiformis*		*C. noctuiformis*	*C. noctuiformis*	*C. noctuiformis*
					C. grotei
Sesia	*S. titan cubensis*	*S. blaini*			
		S. tantalus eumelus			
Pholus	*P. satellitia posticatus*	*P. satellitia satellitia*			*P. satellitia posticatus*
	P. satellitia cinnamomea	*P. vitis hesperidum*			*P. vitis fuscatus*
	P. strenua		*P. strenua*		

TABLE III (*Continued*)

Genus	Cuba	Jamaica	Hispaniola	Puerto Rico	Lesser Antilles
Xylophanes	*X. irrorata* *X. gundlachi*		*X. irrorata*		*X. irrorata*
			X. rhodocera		
	X. porcus *X. chiron cubanus* *X. robinsoni*	*X. jamaicensis* *X. chiron chiron*			*X. chiron lucianus*
Celerio	*C. calverleyi* (?)				

Notes of Special Interest on Table III

1. The Greater Antilles whether they be considered continental fragments broken from Central America or oceanic islands, and the Lesser Antilles or Caribbees, which are certainly oceanic and mostly volcanic in origin, have been so long (in geologic time) separated and insular that many endemic species have arisen, or if not endemic, peculiar to one or more of the islands.
2. Haiti and San Domingo show a close relationship either to Cuba or to Jamaica, with perhaps a closer relationship to Cuba, of the two islands.
3. The smaller islands of the Lesser Antilles have many diversifications owing to their insularity, and strangely enough some of these diversifications such as *Perigonia lusca major* and *Pholus vitis fuscatus*, etc. are larger in size than those of a parent species found on the mainland or on the Greater Antilles, (Cuba, Jamaica, Puerto Rico, Haiti and San Domingo). Haiti and San Domingo are called Hispaniola.
4. The genus *Isognathus* and especially *Isognathus rimosa rimosa*, has no less than five definite sub-species among the Greater and Lesser Antilles. *Phlegethontius rustica* has 3 subspecies, *Erinnyis obscura obscura* occurring as *obscura* on most of these islands if not all, has actually evolved into a wholly new species in Cuba, called *Erinnyis pallida*.
5. Certain species like *Erinnyis ello* and *E. alope*, *Pachylia ficus*, *Xylophanes tersa*, etc. seem to be static and there are few if any varieties or sub-species.

Table IV. Illustrating the Depauperate Sphingidae Fauna of Antilles as Compared with Mexico, Central and South America

Antilles	Central America & Mexico	South America
Herse cingulata	*H. cingulata*	*H. cingulata*
Cocytius cluenthius	*C. cluenthius*	*C. cluenthius*
C. duponchel	*C. duponchel*	*C. duponchel*
C. anteus anteus	*C. anteus medor*	*C. anteus medor*
C. vitrinus		
	C. beelzebuth	*C. beelzebuth*
	C. lucifer	*C. lucifer*
		C. mortuorum
		C. macasensis
Phlegethontius sexta	*P. sexta*	*P. sexta*
P. afflicta	*P. barnesi*	*P. mossi*
P. rustica	*P. quinquemaculata*	*P. afflicta*
P. brontes	*P. dilucida*	*P. dilucida*
	P. kuschei	*P. francescae*
	P. lucetius	*P. lucetius*
	P. diffissa	*P. reducta*
	P. occulta	*P. diffissa*
	P. hannibal	*P. lichenea*
	P. pellenia	*P. floristan*
	P. ochus	*P. hannibal*
	P. crocala	*P. corallina*
	P. lefeburei	*P. perplexa*
	P. rustica	*P. scutata*
	P. albiplaga	*P. clarki*
	P. sesquiplex	*P. tecumana*
	P. muscosa	*P. ochus*
	P. corallina	*P. lefeburei*
	P. lichenea	*P. andicola*
	P. floristan	*P. prestoni*
	P. lanuginosa	*P. stuarti*
		P. rustica
		P. albiplaga
		P. bergi
		P. bergamatypes
		P. armatypes
		P. manducoides
		P. viola-alba
		P. brunalba
		P. leucospila
		P. dalica
		P. carrerasi
		P. vestalis
		P. fosteri
		P. corumbensis
		Chlaenogramma undata
		C. obscura
		C. muscosa

TABLE IV (*Continued*)

Antilles	Central America & Mexico	South America
		Euryglottis albostigmatica
		E. dognini
		E. davidianus
		E. aper
		E. guttiventris
	Dolba clarki	*D. schausi*
	Dolbogene hartwegi	
	D. manni	
	Ceratomia catalpae	
	C. iguana	
	C. hoffmanni	
Nannoparce poeyi		
		Neogene reevi
		N. curitiba
		N. dynaeus
		N. steinbachi
		N. albescens
Sphinx tricolor	*S. merops*	*S. arthuri*
	S. lugens	*S. maura*
	S. geminus	*S. aurigutta*
	S. biolleyi	*S. justiciae*
	S. pseudostigmatica	
	S. separatus	
	S. istar	
	S. praelongens	
	S. lanceolata	
	S. mexicanus	
	S. adumbrata	
	S. libocedrus	
Protambulyx strigilis	*P. strigilis*	*P. strigilis*
P. carteri	*P. xanthus*	*P. eurycles*
		P. fasciatus
		P. euryalis
		P. ockendeni
		P. sulphurea
		P. astygonis
		P. goeldii
Amplypterus gannascus	*A. gannascus*	*A. gannascus*
	A. globifer	*A. dentoni*
	A. donysa	*A. palmeri*
		A. eurysthenes
		A. tigrina
		A. sexoculta
	Trogolegnum pseudambulyx	
	Pachysphinx modesta	
	Monarda oryx	
Pseudosphinx tetrio	*P. tetrio*	*P. tetrio*
Isognathus rimosa rimosa (many subspecies)	*I. rimosa inclitus*	*I. rimosa papayae*
		I. leachi
		I. swainsoni
		I. scyron
		I. menechus
		I. excelsior
		I. australis
		I. allamandae
		I. caricae
		I. mossi

TABLE IV (*Continued*)

Antilles	Central America & Mexico	South America
Erinnyis ello	*E. ello*	*E. ello*
E. alope	*E. alope*	*E. alope*
E. crameri	*E. crameri*	*E. crameri*
E. oenotrus	*E. oenotrus*	*E. oenotrus*
E. obscura	*E. obscura*	*E. obscura*
E. pallida	*E. domingonis*	*E. domingonis*
E. domingonis	*E. yucatana*	*E. lassauxi*
E. guttularis	*E. lassauxi*	
Phryxus caicus		*P. caicus*
Pachylia ficus	*P. ficus*	*P. ficus*
P. syces	*P. syces*	*P. syces*
P. resumens	*P. resumens*	*P. resumens*
		P. darceta
	Klonea babyaga	*K. babyaga*
	Oryba kadeni achemenides	*O. kadeni kadeni*
		O. achemenides
	Leucorhampha triptolemus	*L. triptolemus*
		L. diffusa
		L. ornatus
		L. longistriga
Madoryx pseudothyreus oiclus	*M. oiclus*	*M. oiclus*
	M. pluto	*M. pluto*
	M. bubastus	*M. bubastus*
Hemeroplanes parce	*H. parce*	*H. parce*
	H. nomius	*H. nomius*
	H. pan	*H. calliomene*
		H. grisescens
		H. acuta
	H. inuus	*H. inuus*
H. ramsdeni		
H. jamaicensis		
H. gracilis		
Epistor lugubris	*E. lugubris*	*E. lugubris*
E. latipennis		
E. ocypete	*E. ocypete*	*E. ocypete*
	E. gorgon	*E. gorgon*
	E. taedium	*E. taedium*
		E. bathus
	E. cavifer	*E. cavifer*
	Stolidoptera tachasera	*S. yashasera*
		Protaleuron rhodagaster
	Aleuron carinita	*A. carinita*
		A. ypanemae
	A. chloroptera	*A. cymographum*
		A. chloroptera
	A. iphis	*A. prominens*
	A. neglectum	*A. iphis*
		A. neglectum
	Enyo japix	*E. japix*

TABLE IV (*Continued*)

Antilles	Central America & Mexico	South America
	E. pronoe	*E. pronoe*
	Pachygonia subhamata	*P. subhamata*
	P. caliginosa	*P. caliginosa*
	P. hopfferi	*P. hopfferi*
	P. drucei	
	P. ribbei	*P. ribbei*
Himantoides undata		
Cautethia noctuiformis	*C. spuria*	
	C. yucatana	
		Nyceryx hyposticta
		N. ericea
		N. lunaris
	N. coffeae	*N. coffeae*
		N. magna
	N. tacita	*N. tacita*
	N. eximia	
		N. maxwelli
		N. nictitans
		N. continua
		N. alophus
		N. nephus
	N. riscus	*N. riscus*
		N. stuarti
		N. draudti
	N. mulleri	
		N. clarki
Perigonia divisa		
	P. grisea	*P. grisea*
		P. pallida
P. thayeri	*P. stulta*	*P. stulta*
		P. leucopus
P. lusca	*P. lusca*	*P. lusca*
P. lefebrai		
P. jamaicensis		
P. glaucescens		
	Eupyrrhoglossum sagra	*E. sagra*
	E. corvus	*E. corvus*
		E. venustum
	Sesia ceculus	*S. ceculus*
		S. gehleni
S. blaini		
S. tantalus	*S. tantalus*	*S. tantalus*
S. titan	*S. titan*	*S. titan*
S. fadus	*S. fadus*	*S. fadus*
	Pholus anchemolus	*P. anchemolus*
	P. triangulum	*P. triangulum*
P. satellitia satellitia	*P. satellitia lichaon*	*P. satellitia lichaon*
		P. macasensis
		P. drucei
	P. elisa	*P. neubergeri*
		P. cissi
	P. obliquus	*P. obliquus*
		P. eachus
		P. adamsi

TABLE IV (*Continued*)

Antilles	Central America & Mexico	South America
Pholus (cont.)		*P. translineatus*
	P. typhon	
P. strenua		
P. vitis	*P. vitis*	*P. vitis*
P. fasciatus	*P. fasciatus*	*P. fasciatus*
		P. phorbas
		P. capronnieri
P. labruscae	*P. labruscae*	*P. labruscae*
	Gurelca muelleri	
	G. sonorensis	
	Arctonotus terlooi	
	A. vega	
	Euproserpinus phaeton	
	E. euterpe	
Xylophanes		*X. depuiseti*
	X. adalia	
		X. ploetzi
X. pluto	*X. pluto*	*X. pluto*
	X. tyndarus	*X. tyndarus*
		X. rufescens
X. irrorata		
X. gundlachi		
X. rhodocera		
X. porcus porcus	*X. porcus continentalis*	*X. porcus continentalis*
	X. hannemanni	
		X. schausi
	X. germen	*X. germen*
	X. juanita	
		X. fusimacula
	X. zucheri	
		X. undata
	X. rhodina	
	X. godmani	
	X. falco	*X. xylobotes*
		X. media
	X. ceratomioides	*X. ceratomioides*
		X. guianensis
	X. anubus	*X. anubus*
		X. docilis
		X. amadis
		X. epaphus
	X. acrus	
		X. alegrensis
		X. rothschildia
		X. cosmius
		X. ockendeni
		X. mirabilis
X. chiron chiron		*X. macasensis*
X. chiron nechus	*X. chiron nechus*	*X. chiron nechus*
	X. crotonis	*X. crotonis*
		X. zikani
		X. schreiteri
		X. rhodochlora

TABLE IV (*Continued*)

Antilles	Central America & Mexico	South America
Xylophanes (cont.)	*X. cumedon*	*X. cumedon*
		X. rhodotus
		X. nabuchodonosor
	X. titana	*X. titana*
	X. mulleri	
		X. resta
X. tersa	*X. tersa*	*X. tersa*
		X. suana
	X. turbata	
		X. fosteri
		X. ferotinus
		X. dolius
		X. elara
		X. isaon
		X. hydrata
X. robinsoni	*X. josephinae*	
	X. damocrita	
		X. maculator
		X. aglaor
	X. libya	*X. libya*
	X. loelia	*X. loelia*
	X. neoptolemus	*X. neoptolemus*
		X. pyrrhus
	X. thyelia	*X. thyelia*
	X. jordani	
		Phanoxyla hystrix
Celerio lineata	*Celerio lineata*	*Celerio lineata*
		C. euphorbiarum
		C. annei
C. calverleyi (?)		

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THE SKELETO-MUSCULAR MECHANISM OF THE HEAD AND ABDOMEN OF THE ADULT HORSEFLY [1] (Diptera: Tabanidae)

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Introduction

The blood-sucking flies belonging to the family Tabanidae have long been recognized as serious pests of man and domesticated animals. In connection with their habit of taking blood, they are also known to serve as transmitters of a number of important diseases: certain species of deerflies are vectors of *Loa loa*, and other tabanid flies are said to be able to transmit mechanically tularemia and anthrax. It is not surprising, therefore, that many accounts have been published on various aspects of the anatomy of the female horsefly. Most of these scattered papers are concerned with some phase of the external anatomy of the fly, and many of those which deal with internal organs are extremely superficial in their treatment. The author has found only two papers (Cragg 1912, Cameron 1934) which attempt to present the complete anatomy of the adult horsefly. Cragg's study deals very briefly with some of the conspicuous structural features of *Haematopota pluvialis* and its main value lies in the more detailed account of the head, mouthparts, and alimentary canal. Cameron's valuable paper on the same species emphasizes the gross anatomy of the immature stages and the biology of the species. A study of the literature reveals that there is need for an intensive morphological and histological investigation of both sexes of the horsefly which would provide an adequate background for subsequent experimental studies.

In a recent paper, the author (Bonhag 1949) presented a detailed account of the skeleto-muscular system of the thorax of the adult horsefly. This is the second paper by the author on the anatomy of the horsefly; it proposes to complete the account of the skeleto-muscular system of the head, to analyze in detail the mechanism of feeding, and to investigate intensively the organization of the skeleto-muscular system of the abdomen in both sexes. *Tabanus sulcifrons* Macq. was the main species studied; *T. americanus* Forster was also used in the investigation of the head muscles.

Skeleto-muscular Mechanism

Literature Review

The external anatomy of the head and mouthparts of the female horsefly is well known. Almost every general textbook of entomology includes a discussion of the mouthparts of the horsefly and the scattered references to these structures are too numerous to cite. The publications of Meinert (1881), Patton and Cragg (1913), Bromley (1926) and Snodgrass (1935, 1943) were found most useful in this respect. Nevertheless, it seems necessary to include a comprehensive account of the cuticular parts of the head of the horsefly in the present paper for three reasons. First, the muscle descriptions are more intelligible if they are preceded by a discussion of the cuticular parts to which they are attached; secondly, there is a considerable amount of disagreement in the literature concerning the interpretation of certain areas of the head, and the author wishes to express himself on these points. Finally, a number of new facts about the mouthparts of both sexes are introduced in the discussion.

The literature contains several accounts of the head musculature of the horsefly. Despite the excellence of some of these investigations, there is no single account of the musculature of the head of the horsefly which satisfies all needs. Most of the muscles are in serious need of redescription and the role that these muscles play in the feeding mechanism has not been fully investigated. The male horsefly has been neglected completely by most investigators because this sex does not take blood and is comparatively difficult to obtain. In this paper, the author has attempted to bring together available morphological information on the feeding mechanism of both sexes of the horsefly, to add a considerable body of original information to the record, and to present complete descriptions of all of the muscles of the head and mouthparts of this insect. The following paragraph briefly reviews the work that has been done on the musculature of the head of the horsefly.

Meinert's (1881) early paper on the mouthparts of Diptera made a very valuable contribution to our knowledge of the musculature of the head of the horsefly. Hansen's (1884) excellent paper on the mouthparts of representatives of six families of Diptera has

a section devoted to the muscles of the head of several horseflies. Hansen lists 20 paired muscles and 5 unpaired muscles in the head of *Tabanus* spp. The muscle which Hansen calls "M. adductor claustri salivae" is not present in *T. sulcifrons* or *T. americanus.* There are 5 pairs of muscles in the head of *T. sulcifrons* which Hansen does not include in his account. The illustrations in both Meinert's and Hansen's papers are good; the texts are in Danish. One of the best investigations is that of Berlese (1909) on the genus *Haematopota;* however, his classification of muscles is unwieldy and some of the muscle descriptions are very inadequate. There are several notable omissions in his muscle descriptions including the tentorial adductor of the mandible, the outer retractor of the galea, and levator of the antenna which originates on the frons. The muscles associated with the cibarial and pharyngeal pumps, together with the muscles inserted on the esophagus, are considered by Berlese as pharyngeal muscles and are figured but apparently not described. Berlese deals only with the female and does not discuss the functions of the head muscles in relation to the feeding mechanism. Cragg (1912) has presented an interesting account of the head muscles of *Haematopota pluvialis* which includes most of the muscles present in the female. Unfortunately, many of his descriptions need revision and the illustrations are very poor; in order to get a clear picture of the head muscles from Cragg's figures, it seems necessary to repeat most of the dissections. There are 7 pairs of muscles present in *T. sulcifrons* and *T. americanus* which Cragg does not describe for *Haematopota pluvialis.* In the same paper, Cragg also presents a general account of the mechanism of feeding; this will be discussed later. Patton and Cragg (1913) have published a general account of the head and mouthparts of the female horsefly, based upon Cragg's (1912) paper. More recently, Snodgrass (1935, 1943) and Matheson (1944) have presented interesting accounts of the head and mouthparts of tabanid flies. They have not attempted, however, to treat the musculature in great detail.

In contrast to the amount of work that has been done on the head of the horsefly, the morphology of the abdomen has been very much neglected. The external genitalia of the male horsefly has been briefly described by Cole (1927), Bouvier (1940), and others.

The best account of the external morphology of the abdomen has been published by Bromley (1926). However, much new information has been added by the present author particularly in regard to the intromittent organ of the male and the genital invaginations of the female.

Apparently the musculature of the abdomen and of the external genitalia of the horsefly has never been investigated. Indeed, the abdominal musculature of adult Diptera in general has received scant attention. The author has found that study of the abdominal musculature is a great aid in interpreting the segmentation of the abdomen, the genital invaginations of the female, and the external genitalia of the male. Furthermore, investigation of the musculature is necessary in order to understand the complex mechanism of copulation and insemination.

The Head and Mouthparts

The Head Capsule

From the facial aspect, the head of the horsefly is elliptical in outline with the mouthparts projecting from the ventral part of the head. The head of the male describes a less depressed ellipse than that of the female. The large *compound eyes* occupy the dorsolateral areas of the face. The eyes of the female are distinctly separated from each other along their mesal margins (dichoptic), whereas the eyes of the male are contiguous along the midline of the head (holoptic) (figs. 1 and 2). Each *antenna* is comparatively short and consists of a distinct *scape, pedicel* and *flagellum.* The basal segment of the flagellum is enlarged and bears a spurlike prominence dorsally; the remaining 4 segments are very small. The antennae are inserted in membranous areas of the frons.

The clypeus.—The comparatively large, median sclerite beneath the antennae is the *clypeus;* this can best be seen when the head is viewed from the anteroventral surface (fig. 1). The clypeus is bounded laterally by the *anterior tentorial pits,* dorsally by the strongly arched *clypeofrontal suture,* and ventrally by the labrum. The anterior tentorial pits are contained within the clypeofrontal suture. The clypeal region is divided into three areas by a pair of vertical grooves (*gr*) in the female. Internally these grooves produce a pair of ridges that run lateral to the powerful cibarial

dilator muscles. The clypeus of the male (fig. 2) is somewhat sunken into the lower part of the face and not completely sclerotized as in the female; its median surface is membranous, and the areas of sclerotization coincide with the clypeal areas to which muscle fibers are attached.

Authors have interpreted the clypeal area of the horsefly in different ways. Peterson (1916) has called it the "frontoclypeus" because he believed that it consisted of a fusion of these two areas of the head; his interpretation, logical as it seemed at the time, was based upon the mistaken notion that the strongly arched clypeofrontal suture represented the frontal arms of the "epicranial suture". Recent studies (DuPorte 1946, Snodgrass 1947) have shown that the "epicranial suture" has no morphological validity and that it has frequently been confused with a preformed line of weakness in the cranium which splits at ecdysis. Furthermore, it has been indicated that the "epicranial suture" is usually absent or poorly developed in adult insects which no longer moult. Therefore it seems likely that the "epicranial suture" is absent in the adult horsefly, and that Peterson's interpretation of the clypeus is incorrect. Bromley (1926) has also mistaken the clypeus for the "frontoclypeus" and the same objections may be applied here. Du Porte (1946) has also misinterpreted the clypeal area; he regards it as the "frontoclypeus" but not for the same reasons as the previously mentioned investigators. The main objections to Du Porte's argument is that he disregards the apparently incontrovertible evidence that modified clypeal muscles originate on the inner surface of the area in question. Snodgrass (1944) correctly designates the clypeus in the adult horsefly and has pointed out the relationship between the clypeus and the clypeal muscles (1947). The muscle dissections of the present author confirm Snodgrass' interpretation of the clypeal area in the adult horsefly.

The crux of the matter lies in the problem of whether the modified muscles attached to the supposed clypeal area are truly homologous to the clypeal muscles of more generalized types (in which the frontal and clypeal areas are distinct and unquestioned). Much substantiation has been given to the concept that, in insects, the frontal ganglion and its connectives invariably separate the clypeal and frontal muscles. A lateral dissection of the head reveals that

the dilators of the cibarium of the horsefly are separated from the pharyngeal muscles by the frontal ganglion and its connectives (fig. 10). Thus it seems to follow that the large dilators of the cibarium are homologous to the compressors of the clypeus of orthopteroid forms and that the median sclerite beneath the antennae on the face of the horsefly is the clypeus.

The Frons.—In the past, entomologists have defined the *frons* as the facial area above the clypeus bounded laterally by the frontal arms of the "epicranial suture". As has been pointed out previously, the morphological status of the "epicranial suture" has been discredited (Du Porte 1946, Snodgrass 1947). These authors have also indicated that the frontal arms of this line follow different courses in various insects, i.e. they may pass behind or between the antennae. Therefore, the boundaries of the frons are variable and the term "frons" does not have a definite anatomical meaning. As a result, Snodgrass (1947) proposes that the term "frons" be retained as a convenient descriptive term for the facial area above the clypeus and beneath the vertex. By this definition, the *frons* of the adult horsefly is the comparatively small area above the clypeus, bordered laterally by the mesal margins of the compound eyes and dorsally by the vertex (figs. 1 and 2); it bears the antennae and is divided into halves by a secondary median inflection (*m*) of the cuticula which has been frequently mistaken for the coronal stem of the "epicranial suture". The *dorsal tentorial pits* occur on the lateral areas of the frons; internally these grooves produce the dorsal arms of the tentorium (fig. 5). The slitlike dorsal tentorial pits are adjacent to the clypeus because the latter has apparently expanded dorsally at the expense of the frontal region.

The Vertex.—The narrow strip extending between the mesal margins of the compound eyes and extending over the top of the head is the *vertex* (fig. 1). The "vertex" is another descriptive term which has no precise morphological status because it merely refers to the top of the head, the exact boundaries of which vary in different forms. Nevertheless, it is a term of great convenience. The *vertex* of the male horsefly (fig. 2) is much constricted due to holoptic condition of the eyes; it appears as a line between the mesal margins of the compound eyes except at the top of the head where it is slightly expanded. Internally, however, the vertex of

the male is represented by a pair of wide ridges. Three rudimentary *ocelli* are present on the vertex of both sexes (fig. 11).

The Genae.—The cheek regions or *genae* of the horsefly are the areas of the face between the clypeus and the lower margins of the compound eyes (figs. 1 and 2). The genae extend beneath the head to become confluent with the broad occipital areas of the back of the head.

The Occiput.—The greater part of the concave posterior wall of the head of the horsefly is composed of the occipital areas (figs. 3 and 4). Except for the wedge-shaped *vertex* extending posteriorly over the top of the head, the *occiput* is broadly continuous across the dorsal part of the back of the head.

The Postocciput.—The posterior tentorial pits are points of cuticular invagination in the lower ends of the postoccipital sutures of insects. In the horsefly, the *posterior tentorial pits* are large and open but the postoccipital suture is not clearly defined, although there are submarginal suture-like markings around the occipital foramen which may be the postoccipital suture (fig. 3). There is little doubt, however, that the postocciput is represented by the narrow sclerotized area immediately surrounding the dorsal and lateral margins of the *occipital foramen.* The postocciput is produced dorsally as a vizor-like projection. The postoccipital area was termed the "paroccipu t" by Peterson (1916). In this account the term *paroccipu t* has been restricted to the vizor-like cervical projection of the postocciput (figs. 3 and 4). A pair of *cervical condyles* arise from the postocciput; these condyles articulate with the first cervical sclerites.

The hypostomal bridge.—In the female horsefly, there is a slender, sclerotized piece that extends transversely between the occipital regions, beneath the occipital foramen (fig. 3); this is the *hypostomal bridge.* It is believed that the hypostomal bridge is formed from mesal extensions of the lower occipital regions (postgenae) which eventually meet in some insects to produce a complete bridge. The hypostomal bridge of the horsefly lies above the membranous area in which the basal sclerites of the maxillae and labium are embedded. The *hypostomal bridge* of the male is much broader than that of the female and it almost obliterates the membranous region of the back of the head (fig. 4). Bromley (1926) has expressed

the belief that the cardines and stipites of the maxillae were incorporated into the sclerotized bridge beneath the occipital foramen of the male horsefly. This is erroneous, for the reduced stipites of the male can be found in the ventral membrane of the head. The structure of the male maxilla is discussed in a later paragraph where it will be seen that the reduced stipes of this sex serves as a lever of the maxilla.

The Mouthparts

When the mouthparts are in their normal positions, the *mandibles, maxillae* and *hypopharynx* are contained within the deep groove of the *labium* (fig. 8). The dagger shaped *labrum* covers the labial gutter and its contents. The *maxillary palpi* are carried lateral, and slightly anterior, to the labrum. The labrum, hypopharynx and labium comprise the median mouthparts; the mandibles and maxillae are the paired, lateral organs. The mouthparts of the female are strongly developed for piercing the skin and sucking blood, whereas the mouthparts of the male are not as well developed and they do not take blood.

The Labrum.—The typical labrum of insects consists of a median lobe hanging from the lower part of the face to form the upper lip; the posterior or epipharyngeal wall of the labrum is usually membranous. In the horsefly, the *labrum* is compressed and dagger shaped but has a blunt tip (fig. 1). From the anterior aspect, the labrum is largely sclerotized but the lateral edges are membranous; basally, the labrum of the female bears a median process (*mp*) which projects into the head cavity and upon which a labral muscle is inserted (figs. 10 and 15a). Implanted in the membrane at the base of the labrum, are a pair of small lateral sclerites (*t*) which have been called the tormae (fig. 1). The sclerotized *epipharyngeal wall of the labrum* is excavated along the midline to form the anterior wall of the *food canal* (fig. 8). The labrum of the male is not as long or as strongly developed as that of the female and the proximal, median process of the labrum is lacking.

The Mandibles.—Each of the pointed *mandibles* of the female horsefly is a saberlike organ (fig. 11). The proximal end is stoutly reinforced and bears a *mesal process* and a *lateral process;* the adductor and abductor muscles of the mandible are inserted upon

these processes. The mandibles are attached to the ventral membrane of the head behind the labrum and each articulates with a single *articulatory process* of the head. The mandibles work in a scissor-like fashion and are capable of inflicting a sizable wound; they are absent in the male. The distal half of the cutting edge of each mandible is provided with microscopic teeth (fig. 7a).

The Maxillae.—The bases of the maxillae of the female lie in the membrane of the head beneath the occipital foramen (figs. 3, 11 and 14). The *cardo* is the minute proximal division of the maxilla. Internally the distal end of the cardo is provided with a strong *apodeme* upon which the promotor of the cardo is inserted (fig. 14). The cardo is followed by the larger *stipes* which distally bears the stout *maxillary palpus.* The maxillary palpus of the horsefly is generally regarded as being two segmented. However, the apparent first segment of the palpus may represent the palpifer.[3] The stipes is marked externally by a suture (*x*) which is expressed internally as a ridge (fig. 3). This ridge is continuous with the edge of the galea and serves for the attachment of retractor muscles (fig. 14a). The *galea*[4] is modified into a stylet and bears a series of microscopic recurved spines at its distal end; these can be seen only under high powered magnification (fig. 7b). A small sclerite (*ml*) articulates laterally with the base of the galea and mesally with the base of the hypopharynx (fig. 11).

The maxilla of the male differs considerably from that of the female. As was noted previously, the cardines and stipites are not visible in a posterior view of the head of the male (fig. 4). From the ventral aspect, however, a small sclerite can be seen in the ventral membrane of the head behind the mandible. Internal dissection of the head shows that this sclerite is the lower edge of a lever. The lever represents the reduced *stipes* of the male maxilla (fig. 14c). Apparently, the cardo has been lost. The homolog of the

[3] In those lower Diptera where the maxillary palpus is clearly multisegmented, the levator of the maxillary palpus is attached to the stipes or the palpifer; in the horsefly (fig. 14), a similar muscle is present (*14*) which may indicate the division between the one-segmented palpus and the palpifer. One could not be sure of such an interpretation, however, without the benefit of an intensive comparative study.

[4] Imms (1944) believes that the single stylet of the maxilla of Nematocera is the lacinia. While his argument has much merit, it is not possible to come to a final conclusion at this time. Since the interpretation of this structure does not change the mechanical explanation, the older homology has been used.

promotor muscle of the cardo of the female has been retained, however, and is inserted just above the proximal end of the stipes (fig. 14c, *11*). There are no indications that either the cardines or stipites have fused with the hypostomal bridge in the male horsefly. The *maxillary palpus* is much reduced in the male.

The hypopharynx and salivary pump.—The hypopharynx of generalized insects usually consists of a median, tongue-like lobe suspended from the floor of the head. In the horsefly, the *hypopharynx* is a slender stylet lying posterior to the mandibles (figs. 8 and 10). The *salivary canal* runs through the entire length of the hypopharynx and opens at its apex (fig. 8). Proximally, the hypopharynx is enlarged to form a *salivary pump* activated by dilator muscles originating on the posterior wall of the cibarium (figs. 10 and 15A). A portion of the highly modified proximal end of the hypopharynx extends deeply into the head in the form of a concave plate which forms the posterior wall of the cibarial pump.

The labium.—The labium of the horsefly is superficially similar in appearance to that of the housefly, although less specialized. There is little difference between the labium of the female and male horsefly; it consists of a basal stalk and a pair of distal lobes, the *labella* (figs. 3 and 6). The *labial stalk* is largely membranous and deeply grooved along its anterior surface; the cavity thus formed is the *labial gutter* which contains the mandibular, maxillary and hypopharyngeal stylets (fig. 8). The labial stalk owes its leathery appearance to the numerous, minute spines imbedded in the membrane. The labium is suspended by a membranous base from the posteroventral membrane of the head between the bases of the maxillae. Most of the posterior wall of the labial stalk is occupied by a sclerite called the *theca* (fig. 6). The exact homologies of the labial stalk and the theca are not known, although many have speculated, somewhat fancifully, as to their origin. It is most likely that the theca represents the prementum of the typical labium (Crampton 1942, Snodgrass 1935). Distally the theca produces a pair of articulatory processes (*a*) which do not quite attain the posterior bases of the labella (fig. 6); proximally the theca is forked. A pair of slender sclerites (*b*) on the posterior distal surface of the labial stalk contact the articulatory processes of the theca; each of these slender sclerites in turn loosely articulates distally with a larger, posterior labellar sclerite (*c*). A long slender

arm of this labellar sclerite (*c'*) passes cephalad along the base of the labellum. Each labellum is provided with a lateral sclerite (*d*) upon which a labellar muscle is inserted.

The labella are capable of being spread out over the substratum in such a way that the pads are arranged at right angles to the longitudinal axis of the labial stalk. In this position the labella form a broad disc. The posterior halves of the labella are connected by a membrane but the anterior halves are separated by a deep cleft. Just behind this cleft is a small sclerite with a distinct pointed ridge; this is the *interlabellar sclerite* (fig. 9, *is*). This sclerite may represent the fused glossae, and the labella may be homologous to the paraglossae (Peterson 1916, MacGillivray 1923). On the other hand, Bromley (1926) and Crampton (1942) maintain that the labella are homologous to the labial palpi. The evidence does not conclusively favor either of these arguments. When viewed from the undersurface, the labella are seen to be traversed by a series of minute channels called *pseudotracheae* (fig. 9, *pst*). The exact number of pseudotracheae varies slightly in different individuals of *T. sulcifrons* and there is a tendency for occasional pairs of pseudotracheae to join as they approach the midline. The following figures are averages obtained from 30 female specimens. About 28 pseudotracheae of the posterior half of each labellum empty mesally into a larger *posterior collecting channel* (fig. 9, *pcc*); the posterior collecting channel runs anteriorly to the interlabellar sclerite where the *aperture of the posterior collecting channel* is located (*apcc*). Seventeen *independent pseudotracheae* (*ip*) empty along the mesal edge of the labellum at the sides of the interlabellar sclerite. The remaining pseudotracheae (about 18) of the anterior half of each labellum empty mesally into the *anterior collecting channel* (*acc*) which, in turn, empties through the *aperture of the anterior collecting channel* (*aacc*) into the distal end of the food canal, just before the anterior margin of the interlabellar sclerite. Thus all of the pseudotracheae, either directly or indirectly, empty at the base of the food canal formed by the mouthparts.

The food canal.—Cross sections of the mouthparts of the horsefly show that certain elements form a canal through which liquid food can be drawn up into the sucking pumps and subsequently into

the alimentary canal (fig. 8). It has been known for many years (Vogel 1921) that the anterior wall of the *food canal* is formed by the deeply hollowed out epipharyngeal wall of the labrum. This channel is closed posteriorly by the mandibles and hypopharynx. In the male, the food channel is closed posteriorly by the hypopharynx alone since the mandibles are lacking. The stylets of the maxillae lie behind mandibles.

The Endoskeleton

The inside of the horsefly head is provided with a complex array of cuticular structures:

The tentorium.—The tentorium of the horsefly serves as a strong internal brace of the head capsule and also for muscle attachments (figs. 5 and 11). Each *dorsal tentorial arm* arises from a slitlike dorsal tentorial-pit on the frons and proceeds posteriorly until it meets the coresponding *anterior tentorial arm* near the back of the head (fig. 5). The triangular area (*p*) between the dorsal and anterior tentorial arms is filled in by a thin plate which is formed by an extended inflection of the clypeofrontal suture. The broad *posterior tentorial arm* joins the tentorium in the area where the dorsal and anterior arms meet. At this point, there is a small sclerotized process of the tentorium (*pt*) to which certain neck muscles are attached (Bonhag 1949).

The cibarial pump.—This is the highly modified homologue of the cibarium of more generalized insects; it represents that portion of the preoral space which is posterior to the epipharyngeal wall of the clypeus, anterior to the hypopharynx, and ventral to the *true mouth* (figs. 10 and 15a). The strongly sclerotized, concave, posterior wall of the *cibarial pump* is derived from the proximal end of the hypopharynx—probably the hypopharyngeal suspensorium. The elastic anterior wall of the cibarial pump is usually collapsed against the concave posterior wall and represents the epipharyngeal wall of the clypeus. The cibarial pump bears a pair of processes, the *dorsal cornuae*, to which several important muscles are attached (fig. 10). The cibarial pump of the male is similar to that of the female but not as robustly developed (fig. 12).

The pharyngeal pump.—This cup-like pump lies dorsal to the cibarial pump and is embraced laterally by the *dorsal cornuae* (fig.

10). The cibarial pump opens into the pharyngeal pump by way of the *true mouth* (fig. 15a); the ventral part of the pharyngeal pump is provided with muscles that act as sphincters of the true mouth and constrictors of the pump. When at rest, the dorsal wall of the pharyngeal pump is collapsed into the lumen of the pump (fig. 15a). The male is provided with the same type of pump but it is not as large as that of the female (fig. 12).

The *esophagus* is a narrow tube that leaves the pharyngeal pump at a right angle to the main axis of the food pumps; it is provided with a musculated *valve* near the back of the head (figs. 10 and 15 c).

The salivary pump.—This musculated syringe is provided with a collapsible anterior wall (fig. 15a) and has been mentioned previously in connection with the hypopharynx.

The Muscles of the Head and Mouthparts

The musculature of the head and mouthparts of the horsefly exhibits considerable sexual dimorphism. In the female, the muscles and cuticular parts of the head constitute a highly perfected mechanism for piercing the skin and sucking blood. On the other hand, the males do not take blood but have a feeding apparatus that serves for sucking plant juices. Nevertheless, all of the muscles in the head of the male can be conclusively homologized with muscles present in the female. There are 54 muscles in the head of the female; these consist of 4 unpaired muscles and 25 paired muscles. The head of the male is provided with 46 muscles. The muscles lacking in the male are all paired and consist of: the abductor of the mandible, the outer adductor of the mandible, the tentorial adductor of the mandible, and the outer retractor of the galea. In most cases, the muscles of the head and mouthparts of the male are not as strongly developed as their homologues in the female, and many of them differ somewhat in their origins and insertions.

An intensive study of both sexes clearly indicates that the pattern of muscles in the male has followed a degenerate line of evolution away from the basic plan of head musculature from which the female has developed. Certainly the loss of mandibles and the muscles that activate them can only be regarded as a degenerate specialization. In an earlier part of this paper it was noted that the

maxilla of the male is more specialized than that of the female due to the loss of the cardo and the modification of the stipes into a small lever. The maxillae of both sexes are capable of protraction and retraction only. The fact that the male accomplishes these movements with only two pairs of muscles—whereas the female brings this about with three pairs of separate muscles—is further evidence of specialization by simplification. There are no muscles present in the head of the male that are not also present in the female, except for some migrations of origins and insertions; the muscle pattern in the male can be derived from the ground plan of head muscles in the female by mere subtraction.

The custom of naming the muscles of the head and mouthparts of insects by their functions has become well established in the literature. Although there are a few objections to this system of nomenclature, the author has followed the established precedent. Much care was taken in determining the function of each muscle; this was done by micro-manipulations of muscles in both preserved and freshly killed specimens. The functions of some of the smallest muscles could be determined only by deduction—based upon close observation of the origin, insertion, and axis of movement of each muscle.

The following annotated list of muscles of the head and mouthparts pertains to both sexes of *Tabanus sulcifrons* and *T. americanus*. Unless stated otherwise, each muscle listed is one of a pair of muscles.

1. *Compressor of the labrum* (figs. 10 and 15). A very short muscle arising on the proximal end of the labrum; inserted on the epipharyngeal wall at the base of the cibarial pump. Contraction of this muscle opens the funtional mouth. Present in both sexes.

2. *Retractor of the labrum* (figs. 10 and 15). Median and unpaired in both sexes. In the female, this muscle arises on the clypeus, between the cibarial dilators, and tapers posteroventrad to its insertion on the median, basal process of the labrum. In the male, it is restricted to the upper sclerotized portion of the clypeus and is inserted on the proximal end of the labrum by a long tendon. The tendon-like apodeme flares broadly at its insertion. Probably serves to keep the labrum pressed against the mandibles and hypopharynx.

3. *Depressor of the antenna* (figs. 12 and 13). A very small muscle originating on the dorsal arm of the tentorium and extending anterad to its insertion on the ventral, proximal rim of the scape. Present in both sexes.

4. *Levator of the antenna* (figs. 12 and 13). A minute bundle of fibers originating on the frons of the female near the midline of the head; in the male, this muscle has its origin on the lower end of the ridge which separates the mesal margin of the compound eye from the frons. Inserted, in both sexes, on the dorsal, proximal rim of the scape.

5. *Tentorial levator of the antenna* (figs. 12 and 13). Another small muscle with its origin on the dorsal arm of the tentorium next to the origin of the depressor muscle (*3*); inserted by a small tendon on the dorsal rim of the scape.

6. *Depressor of the flagellum* (fig. 13). Origin on the ventral surface of the scape; insertion on the ventral, proximal lip of the pedicel.

7. *Levator of the flagellum* (fig. 13). Origin on the ventral surface of the scape; insertion on the dorsal, proximal lip of the pedicel.

8. *Abductor of the mandible* (fig. 11). Origin on the back of the head lateral and dorsal to the occipital foramen, inserted by a long tendon on the lateral process of the mandible. Not present in the male.

9. *Outer adductor of the mandible* (fig. 11). A horizontal bundle of fibers originating on the lower genal region and the back of the head; inserted by a stout tendon on the mesal process of the mandible. Not present in the male.

10. *Tentorial adductor of the mandible* (fig. 11). Origin on the tentorium; insertion ventrally on the base of the mesal process of the mandible. This is a robust deltoid muscle (when seen laterally) and is present only in the female.

11. *Promotor of the cardo* (figs. 11 and 14). In the female, a stout bundle of fibers originating on the gena dorsal and lateral to the anterior tentorial pit, tapers to its insertion by an apodeme on the distal end of the cardo. In the male, this horizontal muscle originates on the lower clypeal region (fig. 12), immediately adjacent to the gena, and tapers to its insertion on the reduced stipes

(the cardo has been lost in the male). Contraction of this muscle results in protraction of the galea in both sexes.

12. *Tentorial retractor of the galea* (figs. 11 and 14). This is a short, subcylindrical bundle of fibers in the female; origin on the anterior arm of the tentorium near where the dorsal and anterior tentorial arms join, insertion on a ridge of the stipes which is continuous with the edge of the galea. In the male, the retractor muscle is less robust and tapers to its insertion on the proximal end of the galeal stylet.

13. *Outer retractor of the galea* (figs. 11 and 14). Origin on the back of the head laterad of the origin of the abductor muscle of the mandible (*8*). Inserted by a fine tendon-like apodeme on the ridge on the inner surface of the stipes near the proximal end of the galea. Not present in the male.

14. *Levator of the maxillary palpus* (figs. 12 and 14). A very small band of fibers originating on the ventral wall of the first palpal segment (palpifer?); inserted on the membrane at the dorsal basal rim of the second segment of the maxillary palpus. Present in both sexes.

15. *Retractor of the labium* (figs. 10 and 11). Origin on the back of the head laterad of the occipital foramen; it passes ventrad beneath the tentorium to its insertion on the proximal end of the labium. Present in both sexes.

16. *First extensor of the labellum* (fig. 10). Origin on the inner surface of the theca; inserted on a narrow sclerite (*b*) of the lateroposterior surface of the labium above the labellar lobe. Present in both sexes.

17. *Second extensor of the labellum* (fig. 10). Origin on the inner surface of the theca mesal to the origin of the preceding muscle (*10*); insertion on lateral sclerite (*d*) of the labellum. Present in both sexes.

18. *Flexor of the labellum* (fig. 10). A series of oblique muscle fibers originating on the proximal end of the theca and the lateral surface of the labial stalk; extend anterad to their insertion on the elongate sclerite of the labial gutter (fig. 8). This muscle is attached along the dorsal two-thirds of the anterior wall of the labial stem. Present in both sexes.

19. *Dilator of the cibarial pump* (figs. 10 and 15). A broad band of fibers originating on the lateral area of the clypeus; insertion on the collapsible anterior (epipharyngeal) wall of the cibarial pump. Developed in both male and female.

20. *Retractor of the cibarium* (figs. 10 and 12). An oblique muscle originating on the vertex; passes caudoventrad to its insertion on the dorsal cornua of the cibarial pump. This muscle, in both sexes, is inserted by a long tendon.

21. *Protractor of the cibarium* (figs. 10 and 12). A short bundle of fibers originating on the tentorium (near where the dorsal and anterior arms join); passes dorsad to its insertion on the dorsal cornua of the cibarium. Present in both sexes.

22. *Anterior dilator of the pharyngeal pump* (figs. 10, 12, and 15). Origin on the clypeofrontal ridge at the base of the dorsal arm of the tentorium; extends dorsocaudad to its insertion on the anterolateral surface of the pharyngeal pump. Present in both sexes.

23. *Dorsal dilator of the pharyngeal pump* (figs. 10, 12, and 15). Origin on the vertex between the compound eyes; inserted on the collapsible dorsal wall of the pharyngeal pump. Present in both sexes.

24. *Anterior constrictor of the pharyngeal pump* (figs. 10 and 15). An unpaired muscle consisting of a small band of fibers extending transversely between the dorsal cornuae of the cibarial pump and lying against the anterior surface of the pharyngeal pump.

25. *Posterior constrictor of the pharyngeal pump* (figs. 10, 12, and 15). Similar to the preceding muscle but lies against posterior surface of the pharyngeal pump and is attached to the posterior surface of the dorsal cornua of each side. Present in both sexes and unpaired.

26. *Oblique constrictor of the pharyngeal pump* (figs. 10, 12, and 15). A paired muscle consisting of a minute band of fibers attached dorsally on the posterior surface of the pharyngeal pump, passing obliquely ventrad to its insertion on the same organ. Present in the male and female.

27. *Dorsal dilator of the esophagus* (figs. 10 and 15). A small muscle originating on the back of the head above the occipital fora-

men; passes ventromesad to its insertion on the laterodorsal wall of the esophagus. Present in both sexes.

28. *Lateral dilator of the esophagus* (figs. 10 and 15). Similar to the preceding muscle but originating lower on the back of the head and inserted on the lateroventral surface of the esophagus. In both sexes.

29. *Dilator of the salivary pump* (figs. 10 and 15). A strong bundle of fibers attached anteriorly on the cibarial pump and inserted posteriorly on the collapsible anterior wall of the salivary pump. This unpaired muscle is found in both sexes but is very small in the male.

The Feeding Mechanism

The actions of some of the muscles of the head and mouthparts of the female horsefly have been discussed in relation to the feeding mechanism by Cragg (1912), Patton and Cragg (1913), Snodgrass (1935, 1943), and Matheson (1944). The following discussion is based upon the author's observations in the field and dissections in the laboratory; it attempts to account for the functions of *all* of the muscles of the head and mouthparts of *Tabanus sulcifrons* preparatory to taking blood, while making the wound, and during the process of sucking blood. The functions of the muscles in the male are also considered.

The Female

When the female horsefly alights upon its victim, it frequently palpates the hide of the animal in a wide arc with its extended front legs. Then the head is directed slightly forward and lowered between the extended fore legs. The protracted labium, containing the stylets in the labial gutter, passes between the hairs of the host and touches the skin. At this time, the labella are closed with the pseudotracheal membranes pressed against each other. As the head moves closer to the skin, the maxillary palpus is raised until it becomes porrect; this is brought about by contraction of the levator of the maxillary palpus (fig. 14, *14*).

After the fly has selected a suitable site, the soft labellar pads are spread out over the skin in such a way that they form right angles with the labial stalk. This is accomplished by three pairs of

muscles in the labium (fig. 10): contraction of the paired flexor muscles of the labellum (*18*) draws the apex of the labium (anterior end of the labella) upwards; then, contractions of the first and second extensor muscles of the labellum (*16* and *17*) spread out the labella. It is interesting to note that when the flexor muscles of the labellum (*18*) are relaxed, contraction of the first and second extensor muscles (*16* and *17*) pulls the posterior margins of the labella dorsad and the labella are returned to their folded resting position. When the retractor muscles of the labium (fig. 11, *15*) shorten, the base of the labium is partially withdrawn into the head and the distal ends of the mandibles, maxillae and hypopharynx are exposed.

In many cases, the initial puncturing the skin by the horsefly probably is brought about by the pointed, rigid mandibles aided by a series of short, forward thrusts of the body. Cragg (1912) states that *Haematopota* elevates itself on its hind legs and " gives a series of short jerks forward ". However, the author has observed dozens of *T. sulcifrons* in the act of feeding on cattle and has not been able to detect these forward thrusts with any certainty. Indeed, a simple experiment conducted by the writer indicates that puncturing and laceration of the skin can be brought about directly by the action of the mandibles and maxillae, without a preliminary puncturing of the skin by body thrusts. The evidence is as follows. A large number of *T. sulcifrons* were collected in a wire mesh container and the palm of the hand was placed close to, but not touching, the underside of the container. At the time this collection was made, the horseflies were biting viciously and even attacking man. Many of the horseflies stuck their proboscides through the mesh as far as they could reach. In this restrained position, the horseflies were still able to inflict a painful puncture and in some cases drew blood.

The skin is lacerated by transverse, scissorlike movements of the mandibles and by protraction and retraction of the maxillary stylets (fig. 11). The mandibles are drawn mesad by contraction of the outer, and tentorial adductors (*9* and *10*) and laterad by the action of the abductor of the mandible (*8*). This can be readily understood by studying the disposition of mandibular muscles in figure 11. Some authors state that the mandibles are twisted in the wound; however, manipulations of the mandibular muscles, in both

preserved and fresh specimens, indicate that partial rotation, if it occurs at all, is not one of the cardinal movements of the mandible. Protraction and retraction of each of the maxillary stylets, in the female, are accomplished through an alternate decrease and increase in the outward curvature of the cardo and stipes. Contraction of the promotor muscle of the cardo (*11*) decreases the outward curvature of the cardo and stipes; this pushes the apex of the galea into the skin (fig. 14b). The tentorial and outer retractors of the galea (*12* and *13*) are antagonistic to the promotor of the cardo since, by their simultaneous contraction, they withdraw the galea (fig. 14a). As the mandibles cut deeper into the wound, the head is pressed closer to the skin and the maxillary stylets are retracted and forced farther into the wound. Matheson (1944) suggests that the minute recurved teeth of the maxillae (fig. 7b) "act as holding organs while the mandibles cut deeper and deeper" into the wound. This sounds possible but is difficult to demonstrate.

As a result of the activities of the mandibles and maxillae, the blood begins to flow copiously and is drawn into the food canal by the sucking pumps of the head. Before dealing with the action of these pumps, the role of the labella should be considered. Snodgrass (1935) states categorically that the blood is collected by the pseudotracheae and taken to the food channel formed by the mouthparts. The general similarity between the pseudotracheal membranes of the housefly and the horsefly has been noted by many authors, but apparently no one has located the apertures of the mesal collecting channels in the horsefly. The reader is referred to figure 9 where these apertures are labelled. There are about 17 pseudotracheae (*ip*) on each of the labella which empty independently at the sides of the interlabellar sclerite. The aperture of the anterior collecting channel (*aacc*) opens directly at the base of the food canal. The median ridge of the interlabellar sclerite (*is*) probably directs the flow of fluids, from the posterior collecting channel (*pcc*) and the independent pseudotracheae, towards the food canal. Thus, the pseudotracheal channels of the horsefly appear to be structurely adapted for collecting the exuding blood and directing it to the food canal. However, there is no conclusive evidence that blood is always collected through the pseudotracheal apparatus of the labella when the horsefly feeds.

The food canal is formed by the longitudinal excavation in the labrum and is closed behind by the mandibles and the hypopharynx. The function of the retractor muscle of the labrum (figs. 10 and 15, *2*) has been modified and serves, in the horsefly, to keep the labrum pressed against the mandibles; this holds the food canal intact during feeding.

The blood is sucked up through the food canal by the action of the cibarial dilator muscles (*19*). In the resting position, the anterior wall of the cibarial pump is completely collapsed against the posterior wall. Dilation of the cibarium creates a partial vacuum in its lumen and the blood is drawn up the food canal (fig. 15a). Before this can take place, however, the functional mouth must be opened by contraction of the compressor of the labrum (*1*), and the aperture between the pharyngeal and cibarial pumps (the true mouth) must be closed by contraction of the anterior and posterior constrictors of the pharyngeal pump (*24* and *25*). Under these conditions, the sucking mechanism just described is analogous to that found in a medicine dropper; the cibarial pump would correspond to the rubber bulb and the food canal formed by the mouthparts would correspond to the glass stem.

The next step in the passage of the blood from the wound into the gut is illustrated in figure 15b. Contraction of the anterior and dorsal dilators of the pharyngeal pump (*22* and *23*), synchronized with the relaxation of the anterior, posterior, and oblique contrictors of the pharyngeal pump (*24*, *25*, and *26*), greatly increases the lumen of the pharyngeal pump and opens the true mouth. At the same time, the functional mouth is closed by relaxation of the compressor of the labrum (*1*) and the cibarial pump is collapsed. The anterior wall of the cibarial pump collapses against the posterior wall, when the cibarial dilators relax. Consequently, the blood in the lumen of the cibarium is both pushed and pulled into the pharyngeal pump. The efficacy of the pharyngeal pump is increased by the fact that the esophagus is closed by a valvelike modification of its walls. Thus, when the pharyngeal pump dilates, gases or liquids are not sucked into its lumen from the more posterior regions of the alimentary canal.

Finally, the blood within the pharyngeal pump is forced posterad into the gut by constriction of the pharyngeal pump (fig. 15c).

When the dorsal dilators of the pharyngeal pump (*23*) relax, the dorsal wall of the pump collapses; relaxation of the anterior dilators of the pharyngeal pump (*22*) and contraction of the anterior, posterior, and oblique constrictors of that mechanism (*24*, *25*, and *26*) complete the constriction of the pharyngeal pump. Contraction of the dorsal and lateral dilators of the esophagus (*27* and *28*) unblocks the esophagus and the blood passes farther back into the digestive canal.

Contraction of the powerful cibarial dilator muscles (*19*) tends to pull the system of sucking pumps anterad (fig. 15a). However, simultaneous contraction of the retractor and protractor muscles of the cibarium (fig. 10, *20* and *21*) holds the pump stationary. This contributes to the mechanical efficiency of the cibarium by only allowing the anterior wall to be drawn apart from the posterior wall. Similarly, the large dorsal dilators of the pharyngeal pump (*23*) are prevented from pulling the system of sucking pumps dorsad by a pair of antagonistic muscles, the protractors of the cibarium (*21*). As a result, only the concave, dorsal wall of the pharyngeal pump is elevated (fig. 15b).

The salivary pump is activated by a dilator muscle which originates on the posterior wall of the cibarium (*29*). Contraction of this muscle pulls the thin anterior wall of the pump away from the posterior wall and the salivary secretion is sucked into its lumen (fig. 15a). Relaxation of the same muscle causes the anterior wall of the pump to collapse (fig. 15b). Thus, the lumen of the salivary pump is obliterated and the salivary juice is forced into the salivary conduit which empties at the apex of the hypopharynx.

The Male

The feeding mechanism of the male is similar to that of the female except that the muscles are not as well developed, the mandibles and their muscles are completely absent, and the mechanics of protraction and retraction of the galeal stylet of the maxilla has been considerably modified.

Protraction of the galea in the male is brought about by the homologue of the promotor of the cardo of the female (fig. 14d, *11*): this muscle, by its contraction, pulls the lever-like stipes of the male anterad and forces the galea down into the plant tissue or

other food upon which the insect is feeding. Retraction of the galea is accomplished by contraction of the tentorial retractor of the galea (*12*) and relaxation of the promotor of the cardo (*11*) which restores the stipes to its horizontal position (fig. 14c). The outer retractor of the galea (fig. 14a, *13*) is not present in the male horsefly.

The Abdomen

In this study, the musculature of the horsefly has proved most useful in homologizing the skeletal parts of the abdomen. There are two schools of opinion regarding the value and reliability of muscles in establishing the homologies of the skeletal parts to which they are attached, and contrasting claims have been made. However, this and other studies have convinced the author that, under certain conditions, the abdominal muscles of insects constitute a reliable basis for interpreting cuticular parts of the abdomen. If the muscles in question are serially repeated in the abdominal segments and their origins and insertions are constant, they may be used with considerable assurance in homologizing cuticular parts. Certain muscles in the horsefly are not repeated frequently enough in the abdomen or exhibit certain inconsistencies; these have not been used as primary criteria in determining the relationships of surface areas of the abdomen. The preceding statements will be clarified in the discussion that follows.

Ten segments in the abdomen of both sexes of the horsefly are clearly indicated by the arrangement of serial muscles; the presence of an eleventh segment is suggested by the muscles of the proctiger. Furthermore, the abdominal muscles provide a concrete basis for interpreting the genital and postgenital segments.

The Pregenital Segments

The first seven segments of the abdomen may be termed the pregenital segments because they precede the genital segments and are not modified for sexual purposes. The pregenital segments are the only segments normally visible externally (fig. 16), and are essentially the same in both sexes. The first abdominal segment is the most modified of the pregenital segments because its tergal plate is narrow and because the first and second abdominal sterna

are fused. The arrangement of abdominal muscles and nerves verifies the fact that the first large plate of the venter of the abdomen consists of the fused first and second sternal plates. Each tergal plate of the pregenital area overlaps the succeeding tergal plate, and the same is true of the corresponding sternal plates. The membranous areas between the tergal and sternal plates are usually hidden by the lateral overlapping of the tergal plates but are exposed in fully engorged females. Pulling these plates apart exposes the seven pairs of spiracles in the lateral membranes of the pregenital area.

The Genital Segments of the Female

The genital segments of the female consist of the eighth and ninth abdominal segments (figs. 18 and 20). They are small in size, incompletely sclerotized, and modified for reproductive purposes. Regular organs of oviposition, derived from segmental gonopods, are completely lacking in the horsefly. Except during reproductive activity the genital and postgenital segments are retracted into the seventh abdominal segment (fig. 26). They can be forced out, however, by applying pressure to the base of the abdomen of a specimen that has been treated with potassium hydroxide.

The first genital segment.—The small tergum of the eighth abdominal segment does not overlap its corresponding sternal plate (fig. 18). The sternal plate of the eighth abdominal segment lies in a wide membranous area and extends posteriorly, beyond the caudal limits of the tergum, to form the lobed *subgenital plate* (fig. 21). The muscles attached to the subgenital plate support the view that it represents the eighth abdominal sternum. For example, dorsoventral muscles are present in all of the pregenital segments and are attached to the tergal and sternal plates of their respective segments (fig. 24); this regularly occurring muscle is present in segment eight and is attached dorsally on the tergal plate and ventrally on the subgenital plate (fig. 26, *175*). Another regularly occurring muscle in the pregenital area of the abdomen is the ventral longitudinal muscle. This muscle always has its origin on the anterior end of the sternal plate of the segment to which it belongs, and is inserted on the anterior rim of the succeeding sternal plate

(fig. 24). The ventral longitudinal muscle of the seventh abdominal segment is inserted on the anterior rim of the subgenital plate, leaving no doubt as to the latter's identity (fig. 26, *166*).

The second genital segment.—The ninth segment of the abdomen is even more reduced and modified than the first genital segment. The dorsum is provided with two dorsolateral tergites, separated from each other by a median membranous field (figs. 18 and 20, *tergite IX*); this interpretation is strongly supported by the insertion of the median and lateral dorsal longitudinal muscles of the eighth abdominal segment on the supposed ninth abdominal tergites (fig. 26, *172* and *173*).

Invagination of the region immediately behind the eighth abdominal sternum has carried the sternum of the ninth abdominal segment inward (figs. 18 and 26). The pouch formed by this invagination is the *genital chamber* which leads to the external opening of the median oviduct (fig. 26). The genital chamber receives the intromittent organ of the male during copulation. The *roof of the genital chamber* is formed by the invaginated venter of the ninth abdominal segment and the lateral sclerites of the roof of the genital chamber are sternites of the ninth abdominal segment. When the roof of the genital chamber is viewed dorsally, the lateral sclerites can be seen clearly (fig. 28, *sternite IX*); they turn abruptly mesad and fuse at the anterior end of the genital chamber to form a lyre-shaped sclerite.

Much support can be given to the opinion that the roof of the genital chamber represents the venter of the ninth abdominal segment. The dorsoventral muscles of the ninth abdominal segment are inserted on the lateral sclerites of the roof of the genital chamber (figs. 26 and 28, *183*) and, since these muscles are always inserted on the sternal plates of their respective abdominal segments, the lateral sclerites are undoubtedly sternites of the ninth segment. The posterior attachment of the muscle that seems to be the ventral longitudinal muscle of segment eight (retractor-depressor of the genital chamber) also strengthens this interpretation (figs. 26 and 28, *179*). Finally, sagittal sections of the tip of the abdomen show that the roof of the genital chamber intervenes between the eighth abdominal sternum and the venter of the proctiger (sterna X and XI); thus, the roof of the genital chamber occupies the position,

in the sequence of sternal plates, normally occupied by the ninth abdominal sternum (fig. 20). The fact that a muscle of the eighth abdominal segment has its insertion on the anterior end of the genital chamber (fig. 26, *177*) does not cast doubt upon the opinion that the roof of the genital chamber is the modified venter of the ninth abdominal segment. The muscle in question (*177*) is anomalous and does not have a homologue in any of the other abdominal segments; it may be a modified intersegmental muscle.

The relationships of the genital chamber to the oviducts, the ovaries, the spermatheca, and the accessory glands can be seen in figures 26 and 28. The *spermatheca* presumably arises by secondary invagination of the ectoderm and empties into the roof of the genital chamber; this organ consists of three long tubes that extend anteriorly, bend sharply near their middle, then run posterad. Each tube terminates in a bulbous enlargement. The *accessory glands* consist of two long tubes; each gland is provided with a short duct that empties into the posterior end of the genital chamber. The ducts are closely applied to each other before entering the roof of the chamber.

The Postgenital Segments of the Female

The postgenital segments are the tenth and eleventh abdominal segments which form the anus-bearing, terminal lobe of the abdomen. Authors frequently refer to the postgenital segments collectively as the proctiger. There are only two pairs of muscles in the proctiger of the horsefly but, fortunately, they provide an excellent basis for interpreting this suppressed portion of the abdomen.

The tenth abdominal tergites of the female are situated at the base of the proctiger (figs. 18 and 20, *tergite X*). Proof of their identity is as follows: dorsal longitudinal muscles occur regularly in all of the preceding abdominal segments; in each case, they originate on the tergal plate of the segment to which they belong and are inserted on the anterior rim of the succeeding tergal plate. The ninth abdominal segment of the female horsefly is provided with a pair of dorsal longitudinal muscles, and each of these muscles has its insertion on the assumed tenth abdominal tergites (fig. 26, *182*). Considering the constancy of the muscle involved, the evidence for this interpretation seems highly reliable. By a

similar process of reasoning, the presence of a pair of dorsal longitudinal muscles in the tenth abdominal segment (inserted beneath the bases of the cerci) is strong indication of a rudimentary eleventh segment in the proctiger (fig. 26, *194*). Indeed, it is very likely that the minute lobe, beneath the cerci, which terminates with the anus (*XI?*) represents the eleventh abdominal segment.

There is a considerable amount of disagreement among morphologists as to whether the cerci are appendages of the tenth or eleventh abdominal segments. Embryological evidence seems to favor the idea that the cerci are segmental appendages of the eleventh abdominal segment. In most insects, however, the cerci are activated by muscles of the tenth abdominal segment. In both sexes of the horsefly, the apparent *cerci* seem to be part of the tenth segment and are activated by modified dorsoventral muscles (fig. 26, *196*) presumably belonging to the tenth abdominal segment.

The proctiger is provided with a pair of partially fused ventral plates that certainly include the tenth abdominal sternites and, in all probability, also involve the venter of the eleventh segment (figs. 21 and 26, *sterna X & XI*).

The Genital Segments of the Male

The genital segments of the male are the eighth and ninth abdominal segments. Most authors refer to the ninth abdominal segment as *the* genital segment of male insects and include the eighth segment with the pregenital segments. However, the eighth abdominal segment of the male horsefly is decidedly separated from the pregenital segments and is modified for copulatory purposes. The highly modified ninth segment is provided with clasping organs derived from segmental appendages. The genital and postgenital segments are normally retracted into the seventh abdominal segment.

The first genital segment.—The small, subcrescentic tergal plate of the eighth abdominal segment is surrounded on all sides by membrane (fig. 17 *tergum VIII*); it does not overlap the small corresponding sternal plate (fig. 19). The eighth segment is separated structurely and functionally from the pregenital segments because it is retracted into the pregenital region of the abdomen, together with the ninth and postgenital segments, and is incompletely

sclerotized. Internally, the eighth abdominal segment is modified for copulation; the pattern of muscles of this segment is not like that of a typical pregenital segment and two pairs of these muscles are inserted on the gonocoxopodites of the ninth segment (fig. 27).

The second genital segment.—The ninth abdominal segment of the male is highly modified and complicated by the presence of the copulatory organs; these copulatory organs consist of the intromittent organ and the clasping apparatus. The small dorsolateral tergites are fused with the tergites of the tenth abdominal segment (fig. 19, *tergite IX*). The identity of the ninth tergites is confirmed by the attachment of the dorsal longitudinal muscle of the eighth abdominal segment (fig. 27, *17d*) on the anterior rim of each of the supposed ninth tergites. Furthermore, the ninth tergites articulate laterally with gonocoxopodites which are generally regarded as limb bases of the ninth segment (fig. 19). Comparison with the female, in which the ninth tergites are clearly defined and separated from the tenth tergites (fig. 18), also supports the view that the anterior portions of the compound tergites of the male represent the ninth tergites.

The absence of the ninth sternal plate is difficult to explain. Either the sternal sclerotization of this segment has been suppressed completely in the course of evolution, or the sternal sclerotization has fused with the bases of the claspers. The latter explanation seems most logical and is strongly suggested, but not proven, by the fact that the probable homologues of the ventral longitudinal muscles of the eighth abdominal segment have their posterior attachments on the base of the gonocoxopodites (fig. 27, *18d*). The reader will note that in all of the previous segments, the ventral longitudinal muscle of each segment has its posterior attachment on the sternal plate of the succeeding segment.

The clasping organs.—The morphological interpretation of the copulatory organs of male pterygote insects is in a very unsettled condition at the present time and the homologies have been subjected to many differences of opinion. Some investigators have come to the conclusion that the clasping organs of the male, in some orders of insects, have evolved from phallic structures; others believe that the clasping organs represent the persistent segmental appendages of the ninth abdominal segment. Most phylogenists agree, however, that the clasping organs of the male belong to the

ninth abdominal segment. In the horsefly, the bases of the clasping organs clearly articulate with the ninth tergites and, from their position, appear to belong to the ninth segment. The musculature does not present conclusive evidence, however, since muscles of both the eighth and ninth abdominal segments are inserted on the gonocoxopodites.

Our present knowledge of the comparative morphology of the clasping organs of male insects presents the strongest evidence for interpreting the clasping organs of the horsefly as gonopods of the ninth abdominal segment. Even those authors who maintain that the claspers in some groups of insects are of phallic origin (e.g., Snodgrass, 1935) believe that the clasping organs of Diptera are derived from segmental abdominal appendages. A review of this evidence has been presented by Michener (1944).

The clasping organs of the horsefly consist of the partially fused basal plates of the gonopods (figs. 22 and 29, *gonocoxopodites*) and a pair of movable *gonostyli*. Each gonostylus is activated by adductor and abductor muscles (fig. 30). The gonocoxopodite is the primitive limb basis of the abdominal appendage, and the gonostylus probably represents the telopodite or distal shaft of the segmental appendage. The retention of the styli and their muscles lends further support to the idea that the claspers of the horsefly are segmental appendages.

The intromittent organ.—In its simplest form, the intromittent organ of insects consists of a median, membranous evagination of the posterior wall of the ninth abdominal segment; this is the penis. In the horsefly, the penis has fused with a pair of mesal plates of the gonocoxopodites, the *penis valves*, to form the complex intromittent organ known as the *aedeagus* (figs. 22 and 30). Attached to the base of the aedeagus are a pair of long, slender cuticular rods—the *aedeagal apodemes*. Within the aedeagus is a membranous tube that is apparently formed by invagination of the apex of the aedeagus; this is the *endophallus* into which the *ejaculatory duct* opens (fig. 23). The relationship of the endophallus to the aedeagus, the ejaculatory duct, and the rest of the internal male reproductive organs can be seen in figures 29 and 30. The endophallus of the horsefly is provided with a complex armature upon which a number of important muscles are attached; these sclerites and the associated muscles constitute the mechanism for depositing

the sperm in the female tract during copulation. In order to explain this intricate mechanism, the author has had to apply a series of descriptive terms to the various parts of the endophallic armature. They are:

Endophallic apodeme.—This is a relatively stout, free process of the endophallic armature; it lies beneath the ejaculatory duct and curves slightly ventrad as it extends anteriorly (figs. 22 and 23). Several important muscles are attached to the endophallic apodeme (figs. 29 and 30).

Endophallic guide.—A sclerotized tube, lying free within the endophallus and continuous with the posterior end of the endophallic apodeme (fig. 22). As the endophallic apodeme is protracted by muscle contraction, the endophallic guide is forced to the posterior end of the aedeagus (fig. 23b).

Endophallic hilt.—At the point where the endophallic guide and endophallic apodeme join, there are a short pair of recurved processes resembling the cross guard of a dagger; this region may be called the hilt for descriptive purposes (fig. 23a).

Endophallic tines.—A pair of long, recurved sclerotic prongs attached to the endophalic hilt; they lie free within the endophallus dorsal to the endophallic guide (figs. 22 and 23). Protraction of the endophallic armature forces the ends of the endophallic tines through the opening (phallotreme) at the apex of the aedeagus (fig. 23b).

Endophallic supporting sclerites.—A pair of small sclerites of the wall of the endophallus near the gonopore i.e. at the anterior end of the endophallus; the sclerites are attached to the endophallic tines by narrow hyaline processes and apparently prevent the dorsal wall of the endophallus from collapsing in the region of the gonopore (fig. 23a).

Endophallic guard.—This sclerite is applied to the dorsal and lateral walls of the endophallus and is fixed to the ventrolateral walls of the aedeagus by a pair of lateral processes (fig. 23a). It is shield-shaped when seen from above (fig. 30). The endophallic guard remains stationary as the endophallus is being retracted and protracted. Since the endophallic walls are attached to the guard sclerite, the latter prevents the endophallus from being completely everted during protraction.

The Postgenital Segments of the Male

The postgenital segments (X and XI) form the anus-bearing lobe above the external genital organs (fig. 27). The dorsal longitudinal muscles of the ninth and tenth abdominal segments are lacking in the male and, therefore, cannot be used to homologize the terga of the tenth and eleventh segments as they were in the female. Direct comparison of the male with the female, however, establishes the homologies of most of the parts of the proctiger. The tenth abdominal tergites of the male are fused with the ninth tergites (compare figures 18 and 19, *tergite IX* and *tergite X*). The *ventral plates of the proctiger* (figs. 19, 22, and 27) probably represent the fused sternites of the tenth and eleventh segments. As in the female, the small lobe beneath the *cercus,* terminating with the anus, probably represents the eleventh abdominal segment (fig. 27, *XI?*).

The Abdominal Muscles

There are 141 muscles in the abdomen of the female consisting of 70 paired muscles and 1 unpaired muscle; the male horsefly has 154 abdominal muscles comprising 76 paired muscles and 2 unpaired muscles. Sexual dimorphism in the abdominal musculature of the horsefly is exhibited not only by the muscles of the genital segments but is also found in the musculature of some of the pregenital segments (i.e. segments V, VI, and VII). The type of sexual dimorphism found in the musculature of the abdomen differs from that found in the head in several ways. The reader will recall that the male horsefly has fewer muscles in the head than the female, and that all of the muscles present in the head of the male may be conclusively homologized with muscles in the female. Furthermore, it was stated earlier in this paper that the musculature of the head of the male can be derived from the ground plan of the head muscles of the female by mere subtraction. No such simple analysis can be offered for the abdominal musculature of both sexes of the horsefly.

The initial impression of the abdominal musculature is that of bewildering complexity, particularly in regard to the genital segments. Upon closer analysis, however, it was found that a basic plan of musculature pervaded the abdominal segments. This basic

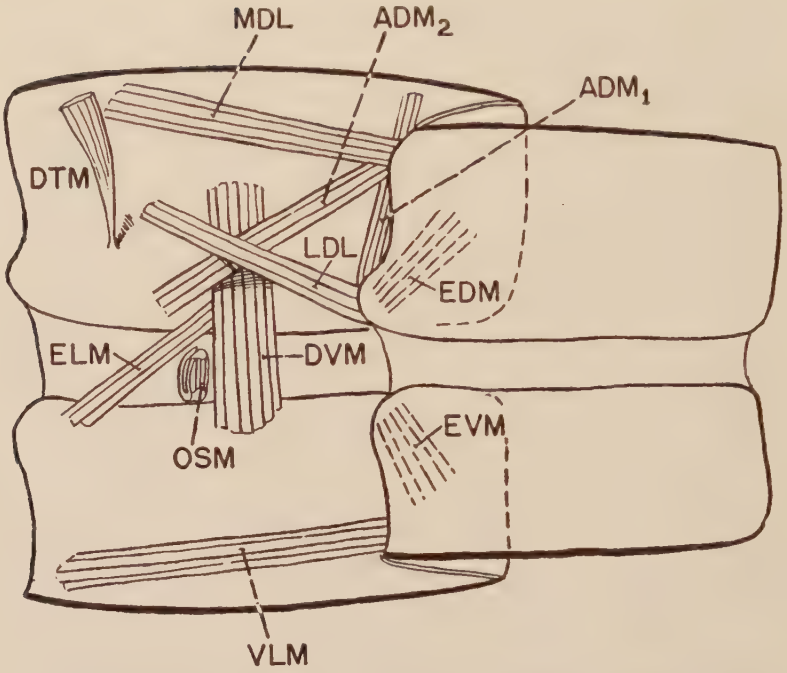
plan is followed rather closely in the pregenital segments; it is modified considerably in the genital segments by the loss of certain muscles and by the presence of special muscles associated with the internal and external genital organs. The musculature of the postgenital region of the abdomen is greatly suppressed. In the female, however, there is good evidence that the muscles of the postgenital region are remnants of the ground-plan musculature of the pregenital segments.

Since the musculature of all of the abdominal segments of the horsefly has probably evolved from a single basic plan, reconstruction of this generalized plan would be of great value in interpreting the present pattern of muscles in each of the abdominal segments. Unfortunately it is impossible to do exactly that from the muscles remaining in the abdomen of the horsefly, but an approximation of the generalized condition can be obtained by summarizing the existing muscle pattern in both sexes and constructing a composite pregenital segment. This method of approach has been used in the following discussion. Each of the abdominal segments of both sexes has been compared with the formulated pregenital segment.

The Musculature of a Typical Pregenital Segment

The basic arrangement of muscles in a typical pregenital segment of the horsefly is relatively simple and consists entirely of paired muscles (text figure 1). These may be conveniently grouped into dorsal muscles, lateral muscles, ventral muscles, transverse muscles, and spiracular muscles.

The dorsal muscles consist of the median dorsal longitudinal muscles, (*mdl*), the lateral dorsal longitudinal muscles, (*ldl*), the accessory dorsal muscles, (adm_1), the second accessory dorsal muscles, (adm_2), and the external dorsal muscles, (*edm*); these muscles all have their origins and insertions on tergal structures. The median, lateral, and external dorsal longitudinal muscles are repeated in most of the pregenital segments of both sexes and are unquestionably elements of the ground-plan musculature of the pregenital area of the horsefly. The accessory dorsal muscles occur in the fifth, sixth, and seventh abdominal segments of the male, and the second accessory dorsal muscles occur only in the sixth and seventh segments of the male; inasmuch as these muscles are sepa-



Text figure 1.—Musculature of right half of typical pregenital segment of *T. sulcifrons*, based upon both sexes. ADM_1, accessory dorsal muscle; ADM_2, second accessory dorsal muscle; DVM, dorso-ventral muscle; DTM, dorsal transverse muscle; EDM, external dorsal muscle; ELM, external lateral muscle; EVM, external ventral muscle; LDL, lateral dorsal longitudinal muscle; MDL, median dorsal longitudinal muscle; OSM, occlusor of spiracle; VLM, ventral longitudinal muscle.

rate, distinct, and serially disposed in the posterior pregenital segments of the male, the author believes that they were once part of the generalized pregenital musculature of both sexes, and were later lost in the female.

The lateral muscles of the typical pregenital segment extend between the tergal and sternal plates. They consist of the dorso-ventral muscles (*dvm*), which are regular features of the pregenital segments of both sexes, and the external lateral muscles (*elm*) which are serially repeated in the fifth through seventh abdominal segments of both sexes. The latter muscle also occurs in the fourth abdominal segment of the female.

The ventral muscles of the typical pregenital segment have their origins and insertions on sternal plates. The ventral longitudinal muscles (*vlm*) are extremely constant and occur in all of the pregenital segments of the horsefly. The external ventral muscles (*evm*) are repeated in the second through seventh segments of the female and the second through sixth segments of the male.

The transverse muscles of the abdomen comprise the dorsal and ventral transverse muscles. The former (*dtm*) arise on the tergum, are attached to the heart, and the fibers of the latter (not figured) are scattered through the ventral diaphragm. The spiracular occlusor muscles (*osm*) occur in all of the pregenital segments of both sexes.

To recapitulate, a typical pregenital segment has been constructed which includes all of the regularly occurring muscles of both sexes of the horsefly with the belief that the resulting muscle pattern approximates, to a certain extent, the basic ground plan of musculature from which each of the abdominal segments has evolved. This generalized scheme of pregenital musculature is not intended to represent a complete reconstruction of the ancestral type, but merely attempts to present a simple pattern of muscles which will be useful in analyzing the musculature of the abdominal segments of the horsefly by making the differences and similarities between segments more apparent.

The Abdominal Muscles of Both Sexes Compared

The muscles of the base of the abdomen of the male and female are alike. The musculature of this region of the body (fig. 24) differs from that of the typical pregenital segment by the presence of a pleurosternal muscle (*109*) originating on the metepimeron and the lateral thoracico-abdominal muscle (*110*); these muscles do not have homologues in any of the succeeding pregenital segments. A reversed tergosternal muscle (*111*) is present and is probably homologous to the dorsoventral muscle of the formulated pregenital segment. The external dorsal, the external lateral, and the external ventral muscles of the typical pregenital segment are lacking; the same is true of the accessory and second accessory dorsal muscles (cf. text figure 1). The loss of the external ventral muscle is compensated for in function by the reversal of the tergosternal muscle.

The second through fourth abdominal segments have very similar muscle patterns in the two sexes (fig. 24). The second segment lacks the accessory and second accessory dorsal muscles, the external lateral muscles, and the dorsal transverse muscles of the typical pregenital segment (text figure 1). The third abdominal segment lacks the accessory dorsal and second accessory dorsal muscle, and the external lateral muscles. The fourth abdominal segment of the female differs from the typical pregenital segment only by the absence of the accessory dorsal and second accessory dorsal muscles; besides these, the fourth segment of the male also lacks the external lateral muscle.

The fifth abdominal segment of the male differs from the typical pregenital segment only by the loss of the second accessory dorsal muscle (fig. 25, *cf.* text figure 1), and the female has a nearly complete complement of muscles in this segment except that the accessory dorsal muscles and the second accessory dorsal muscles are lacking (fig. 24). The sixth abdominal segment has a complete complement of muscles except that external ventral muscles have been lost in the male (fig. 25), and the accessory and second accessory dorsal muscles are absent in the female (fig. 24). Thus the reader will note that the complete complement of muscles, in relation to the formulated pregenital musculature, is approached as one works posteriorly towards the genital segments. Generally speaking, the male has a more complete set of abdominal muscles than the female. The first six pregenital segments show no special modifications of the musculature for reproductive functions, but the retention of a more complete set of muscles in the fourth through sixth abdominal segments in both sexes is correlated in part with the greater mobility of the posterior half of the abdomen during mating and oviposition.

The seventh abdominal segment of the male resembles the typical pregenital segment but lacks the external dorsal and external ventral muscles (fig. 27, *cf.* text figure 1). On the other hand, the seventh segment of the female is modified by the loss of the external dorsal, external ventral, accessory dorsal, and second accessory dorsal muscles (fig. 26); also, three pairs of muscles originate on the seventh segment and are inserted on the oviducts. These muscles are: the protractor of the oviduct (*167*), the retractor of

the oviduct (*168*), and the constrictor of the oviduct (*169*). No homologues of these muscles exist in any of the other abdominal segments of the horsefly.

The musculature of the eighth abdominal segment of the female shows several striking points of similarity with that of the typical pregenital segment (fig. 26, *cf.* text figure 1). These points of similarity are so important that it seems safe to assume that the musculature of the first genital segment has evolved from a basic ground plan not unlike that of the pregenital area. For example, the median dorsal longitudinal muscles (*172*), the lateral dorsal longitudinal muscles (*173*), and the dorsoventral muscles (*175*) are typically developed in the eighth segment (fig. 26). Furthermore, the retractor-depressor of the genital chamber (*179*) is probably homologous to the ventral longitudinal muscle of the pregenital segments; note that this muscle has its origin on the anterior end of the eighth sternal plate and is inserted on the roof of the genital chamber (ninth sternum). The three pairs of special muscles which do not have homologues in the pregenital segments are inserted on the genital chamber; they include the tergal protractor of the genital chamber (*177*), the sternal protractor of the genital chamber (*178*), and the retractor of the genital chamber (*181*).

The musculature of the eighth abdominal segment of the male has been reduced to 4 pairs of muscles (fig. 27); it is significant that 2 pairs have homologues in the typical pregenital segment, and that a third pair may be homologous to the ventral longitudinal muscles of the pregenital segments. The dorsal longitudinal muscle of the male (*174*) definitely has a homologue in the pregenital segment but one cannot be sure of whether it is the median or lateral dorsal longitudinal muscle. The dorsoventral muscle (*175*) is unquestionably homologous to the muscle of the same name in the typical pregenital segment. The sternal retractor of the gonocoxopodite (*180*) may be homologous to the ventral longitudinal muscle (if the ninth sternum has fused with the gonocoxopodites). Only the anterior tergal muscle of the gonocoxopodite (*176*) of the eighth abdominal segment completely defies interpretation.

There are only 2 pairs of abdominal muscles remaining in the ninth abdominal segment of the female (fig. 26). The dorsal longitudinal muscles (*182*) are homologous to either the median

or lateral dorsal longitudinal muscles of the typical pregenital segment. The dorsoventral muscles (*183*) of the ninth segment have been modified to form the dilators of the genital chamber, but are undoubtedly homologous to the dorsoventral muscles of the pregenital segments (the roof of the genital chamber represents the venter of the ninth segment).

The musculature of the ninth abdominal segment of the male least resembles that of the typical pregenital segment (fig. 27). The only homologue present is the dorsoventral muscle (*183*) and, even in this case, the muscle appears so modified that the homology is not certain. All evidence seems to indicate that the clasping organs of the horsefly are segmental appendages of the ninth abdominal segment. The posterior tergal muscles of the gonocoxopodite (*184*) probably represent remnants of the muscles of the limb basis that have long since disappeared from the other segments of the abdomen. The same is probably true of the intrinsic muscles of the gonocoxopodite (fig. 30, *186, 187,* and *188*). The remaining muscles are associated with the aedeagus and are concerned with protraction and retraction of the endophallic armature during the process of insemination. In the light of our present knowledge, the homologies of the muscles of the intromittent organ are obscure.

The proctiger of the horsefly is the terminal lobe of the abdomen consisting of the tenth abdominal segment and, in all probability includes the eleventh abdominal segment. The dorsal longitudinal muscle of the tenth segment of the female (fig. 26, *194*) is homologous to either the median dorsal or lateral dorsal longitudinal muscle of the typical pregenital segment. Its presence and nature of insertion indicates that the eleventh segment is the anus-bearing lobe beneath the cercus (fig. 26). The dorsoventral muscle of the cercus (*196*) may be homologous to the dorsoventral muscle of the typical pregenital segment. This muscle is also present in the male. The dorsal longitudinal muscle of the tenth segment is lacking in the male. The lateral oblique muscle of the proctiger (*195*) is present only in the male and its interpretation seems impossible at this time.

Annotated List of Abdominal Muscles

The author presented an annotated list of muscles of the head and mouthparts of the horsefly in the first section of this paper, and in a previous publication (1949), described the muscles of the thorax. The muscles in the head and thorax were totaled and numerical designation of the abdominal muscles was continued from that figure. A discrepancy of two muscles will be noted; this is due to the fact that the author has adjusted the total number of thoracic muscles.[5]

All of the muscles of the abdomen of both sexes of *Tabanus sulcifrons* are described in the following pages. Each muscle described is one of a pair unless stated otherwise.

Muscles of the Base of the Abdomen (fig. 24)

107. *Median dorsal longitudinal muscle.* A short band of fibers originating on the metathoracic postnotum and extending caudad to its insertion on the anterior rim of the second abdominal tergum. Present in both sexes.

108. *Lateral dorsal longitudinal muscle.* A short sheet of oblique fibers attached anteriorly on the first abdominal tergum; inserted on the anterior margin of the second abdominal tergum. Similar in both sexes.

109. *Pleurosternal muscle.* A narrow muscle originating on the metepimeron and extending caudad to its insertion on the anterior corner of the first sternal plate of the abdomen. Present in both sexes.

110. *Lateral thoracico-abdominal muscle.* A long series of short fibers originating on the metepimeron and inserted along the anterolateral rim of the first abdominal tergum. Present in female and male.

111. *Reversed tergosternal muscle.* Attached dorsally to the anterior corner of the first abdominal sternal plate, passes posteroventrad to its attachment on the lower edge of the first abdominal

[5] The coxosubalar muscle (Bonhag 1949, *39*) was not reported as being present in the mesothorax of the horsefly but was given a number because it had been described in other Diptera. A ventral longitudinal muscle (*43*) was reported in the thorax of the horsefly; subsequent dissections have convinced the author that this muscle does not exist as such.

tergum. This muscle is hidden in a sagittal section by the overlapping of the first sternal plate. Similar in both sexes and probably homologous to the dorsoventral muscles of the succeeding abdominal segments.

112. *Ventral longitudinal muscle.* Origin on the sternal apophysis of the metathorax; insertion on anterior end of the compound first sternal plate of the abdomen. Present in female and male.

113. *Occlusor of the spiracle.* A very small vertical muscle of the first abdominal segment. Attached at both ends of the spiracle. In both sexes.

114. *First dorsal transverse muscle* (not figured). An indistinct group of muscle fibers originating on the mesothoracic phragma and inserted on the first chamber of the heart.

Muscles of the Second Abdominal Segment (fig. 24)

115. *Median dorsal longitudinal muscle.* Origin on the second abdominal tergum; insertion on the anterior rim of the third abdominal tergum. Present in both sexes.

116. *Lateral dorsal longitudinal muscle.* An oblique band of fibers originating on the posterolateral surface of the second abdominal tergum, passes posteroventrad to its insertion on the anterior corner of the third tergal plate. Observed in both sexes.

117. *External dorsal muscle.* A band of short fibers hidden by the overlapping of tergal plates. Originates posteriorly on the second abdominal tergum; inserted anteriorly on the anterior rim of the third abdominal tergum. This reversed muscle is present in both sexes.

118. *Dorsoventral muscle.* A vertical muscle located posterior to the second abdominal spiracle in both male and female. Attached dorsally on the second abdominal tergum; attached ventrally on the compound first sternal plate.

119. *Ventral longitudinal muscle.* Origin on the posterior half of the compound first sternal plate. Inserted on the anterior rim of the third abdominal sternum. Also present in the male.

120. *External ventral muscle.* An oblique band of reversed fibers originating posteriorly on the compound first sternal plate, passes anterodorsad to its insertion on the anterior corner of the

third abdominal sternum. Hidden by the overlapping of the abdominal segments. In both sexes.

121. *Occlusor of the second abdominal spiracle.* Similar to *113.*

Muscles of the Third Abdominal Segment (fig. 24)

122. *Median dorsal longitudinal muscle.* Similar to *115.*
123. *Lateral dorsal longitudinal muscle.* Similar to *116.*
124. *External dorsal muscle.* Similar to *117.*
125. *Dorsoventral muscle.* Similar to *118.*
126. *Ventral longitudinal muscle.* Similar to *119.*
127. *External ventral muscle.* Similar to *120.*
128. *Occlusor of the spiracle.* Similar to *113, 121.*
129. *Dorsal transverse muscle.* A petiolate bundle of muscle fibers originating on the tergum, anterior to the dorsoventral muscle, extends dorsomesad and fans out to its attachment on the heart. Present on both sexes.

Muscles of the Fourth Abdominal Segment (fig. 24)

130. *Median dorsal longitudinal muscle.* Similar to *115.*
131. *Lateral dorsal longitudinal muscle.* Similar to *116.*
132. *External dorsal muscle.* Similar to *117.*
133. *Dorsoventral muscle.* Similar to *118.*
134. *External lateral muscle.* This small muscle is very weakly developed in the fourth abdominal segment of the female and consists of only a few fibers. Origin on the anterior corner of the fourth sternal plate and extends posterodorsad before the spiracle; inserted on the fourth tergal plate beneath the dorsoventral muscle. Very difficult to find in the female and apparently absent in the male.
135. *Ventral longitudinal muscle.* Similar to *119.*
136. *External ventral muscle.* Similar to *120.*
137. *Occlusor of the spiracle.* Similar to *113.*
138. *Dorsal transverse muscle.* Similar to *129.*

Muscles of the Fifth Abdominal Segment (figs. 24 and 25)

139. *Median dorsal longitudinal muscle.* Similar to *115.*
140. *Lateral dorsal longitudinal muscle.* Similar to *116.*
141. *External dorsal muscle.* Similar to *117.*

142. *Accessory dorsal muscle* (fig. 25). A nearly vertical muscle originating on the posterior part of the fifth abdominal tergum; extends ventrad to its insertion on the anterior corner of the sixth abdominal tergum, near the insertion of the lateral dorsal longitudinal muscle (*140*). Present only in the male.

143. *Dorsoventral muscle.* Similar to *118.*

144. *External lateral muscle.* Similar to *134* but slightly more developed.

145. *Ventral longitudinal muscle.* Similar to *119.*

146. *External ventral muscle.* Similar to *120.*

147. *Occlusor of the spiracle.* Similar to *113.*

148. *Dorsal transverse muscle.* Similar to *129.*

Muscles of the Sixth Abdominal Segment (figs. 24 and 25)

149. *Median dorsal longitudinal muscle.* Similar to *115.*

150. *Lateral dorsal longitudinal muscle.* Similar to *116.*

151. *External dorsal muscle.* Similar to *117.*

152. *Accessory dorsal muscle* (fig. 25). Serially homologous to *142.* Origin on the posterior part of the sixth abdominal tergum, passes anteroventrad to its insertion on the anterior margin of the seventh abdominal tergum. Present in the male only.

153. *Second accessory dorsal muscle* (fig. 25). Origin on the sixth abdominal tergum, just dorsal to the spiracle; extends posteromesad to its insertion on the anterior rim of the seventh abdominal tergum. Present in the male only.

154. *Dorsoventral muscle.* Similar to *118.*

155. *External lateral muscle.* Present in both sexes. Origin on the anterior corner of the sixth abdominal sternum; passes in front of the spiracle to its insertion on the sixth abdominal tergum.

156. *Ventral longitudinal muscle.* Similar to *119.*

157. *External ventral muscle* (fig. 24). Similar to *120* in the female; this muscle has not been observed in the male.

158. *Occlusor of the spiracle.* Similar to *113.*

159. *Dorsal transverse muscle.* Similar to *129.*

Muscles of the Seventh Abdominal Segment

160. *Median dorsal longitudinal muscle* (figs. 26 and 27). Origin on the seventh tergum near its anterior margin, passes

mesad and posterad to its insertion on the anterior rim of the eighth tergal plate. Present in both sexes.

161. *Lateral dorsal longitudinal muscle* (figs. 26 and 27). Origin on the seventh abdominal tergum, laterad of the median dorsal longitudinal muscle, extends obliquely posterad to its insertion on the anterior edge of the eighth abdominal tergum. In the male, this muscle originates on the anterior corner of the seventh abdominal tergum and passes horizontally posterad to its insertion on the " horn " of the subcrescentic eighth tergum.

162. *Accessory dorsal muscle* (fig. 27). Origin dorsally on the posterior part of the seventh abdominal tergum; extends ventrad to its insertion on the eighth tergum, next to the insertion of the preceding muscle (*161*). Serially homologous to *152* and present in the male only.

163. *Second accessory dorsal muscle* (fig. 27). Origin on the seventh tergal plate near the spiracle. Extends posterodorsad and mesad to its insertion on the anterior margin of the eighth tergum. Absent in the female. Serially homologous to *153*.

164. *Dorsoventral muscle* (figs. 26 and 27). A broad lateral sheet of muscle fibers that can be seen when the eighth segment is drawn caudad. Attached dorsally on the tergum of the seventh abdominal tergum and attached ventrally on the seventh abdominal sternum. Present in both sexes.

165. *External lateral muscle* (figs. 26 and 27). The most strongly developed external lateral muscle of the abdomen. Attached ventrally on the anterior corner of seventh abdominal sternum, passes obliquely posterad (before the spiracle) to its dorsal attachment on the seventh abdominal tergum. Present in both sexes.

166. *Ventral longitudinal muscle* (figs. 26 and 27). Origin on the anterior margin of the seventh sternum; passes caudad to its insertion on the anterior rim of the eighth abdominal sternum. Present in both sexes.

167. *Protractor of the oviduct* (fig. 26). Functions to pull the oviduct caudad. Origin near the midline of the posterior part of the seventh abdominal sternum, extends anterolaterad to the undersurface of the oviduct. A paired muscle that is sometimes difficult to distinguish. No homologue of this muscle in the male.

168. *Retractor of the oviduct* (fig. 26). A small group of loose muscle fibers originating at the anterior end of the seventh sternum, laterad of *166;* the fibers fan out and penetrate the walls of the lateral oviduct. No homologue present in the male.

169. *Constrictor of the oviduct* (fig. 26). A loose bundle of fibers originating on the posterior part of the seventh abdominal sternum, near the origin of *167,* passes anterad to the major folds at the base of the median oviduct; it forms a loop around the base of the oviduct with the muscle of the other side. Inconspicuous and difficult to find. No homologue in the male.

170. *Occlusor of the spiracle* (figs. 26 and 27). Similar to *113.*

171. *Dorsal transverse muscle* (figs. 26 and 27). Similar to *129.*

Muscles of the Eighth Abdominal Segment

172. *Median dorsal longitudinal muscle* (fig. 26). A relatively broad muscle originating on the anterior surface of the eighth abdominal tergum; inserted on the membrane at the anterior edge of the ninth abdominal tergite. Present in the female.

173. *Lateral dorsal longitudinal muscle* (fig. 26). A relatively long, slender muscle originating on the anterior surface of the eighth abdominal tergum, laterad of the preceding muscle (*172*); passes posteroventrad to its insertion on the lower edge of tergite nine. Apparently lacking in the male.

174. *Dorsal longitudinal muscle of the male* (fig. 27). This muscle originates on the anterior rim of the subcrescentic eighth tergite and extends posterad to its insertion on the anterior margin of the ninth tergite. Probably homologous to the median dorsal longitudinal muscle of the female (*172*).

175. *Dorsoventral muscle* (figs. 26 and 27). A vertical sheet of fibers attached dorsally on the eighth tergum in both sexes. In the female this muscle originates on the lower edge of the tergal plate and the fibers converge to their ventral attachment on the anterior corner of the eighth abdominal sternum (fig. 31). In the male, the muscle is broadly attached to the inner surface of the eighth sternum.

176. *Anterior tergal muscle of the gonocoxopodite* (fig. 27). This is a relatively powerful muscle for which there is no homo-

logue in the female. Origin on the eighth tergite mesad and posterad to the origin of the dorsoventral muscle (*175*); the fibers extend ventrad and slightly anterad to their insertion on the undersurface of the fused gonocoxopodites (fig. 29).

177. *Tergal protractor of the genital chamber* (fig. 26). Present in the female only. Functions to draw the genital chamber posterad. A slender muscle originating on the posterior rim of the eighth tergum, extends anteroventrad to its insertion on the anterior end of the lateral sclerite of the roof of the genital chamber (fig. 28).

178. *Sternal protractor of the genital chamber* (figs. 26 and 31). Origin on the posterior end of the eighth abdominal sternum of the female, near the midline; passes anterad and laterad to its insertion on the lateral sclerite of the roof of the genital chamber next to the insertion of the succeeding muscle (*179*). Contraction of this muscle pulls the genital chamber posterad.

179. *Retractor-depressor of the genital chamber* (fig. 26). Origin on the anterior corner of the eighth abdominal sternum of the female (fig. 31), runs posterodorsad to its insertion at the sides of the roof of the genital chamber (fig. 28). Since the roof of the genital chamber is homologous to the venter of the ninth abdominal segment, this muscle is probably serially homologous to the ventral longitudinal muscles of the preceding segments (*112, 119, 126, 135,* etc.).

180. *Sternal retractor of the gonocoxopodite* (figs. 27 and 29). A short, stout bundle of fibers originating on the anterior rim of the eighth sternite of the male, extends posteromesad for a very short distance to its insertion on the ventral surface of the gonocoxopodite near the midline. This muscle may represent the ventral longitudinal muscle of the ninth abdominal segment of the male. Possibly homologous to *179* in the female.

181. *Retractor of the genital chamber* (figs. 26 and 31). Present only in the female. A broad, horizontal, unpaired bundle of fibers originating on the anterior end of the eighth abdominal sternum. Insertion on the floor of the genital chamber. Contraction of this muscle pulls the genital chamber anterad.

Muscles of the Ninth Abdominal Segment

182. *Dorsal longitudinal muscle* (fig. 26). A very small muscle originating on the anterior rim of the ninth abdominal tergite; inserted on the anterior margin of the tenth abdominal tergite. Not present in the male.

183. *Dorsoventral muscle* (figs. 26 and 27). In the female, this muscle has been modified to serve as the dilator of the genital chamber. Origin on the ninth abdominal tergite, passes ventrad to its insertion on the lateral sclerite of the roof of the genital chamber (fig. 28). The roof of the genital chamber represents the venter of the ninth segment and the lateral sclerites are sternites of that segment. This muscle in the female is clearly homologous to the dorsoventral muscles of the preceding abdominal segments. In the male, the muscle that appears to be homologous to the dorsoventral muscle of the ninth segment is highly modified (fig. 27); it originates on the ninth tergite but is inserted on the posterior end of the ventral plate of the proctiger.

184. *Posterior tergal muscle of the gonocoxopodite* (fig. 27). Originates dorsally on the ninth tergite of the male and extends ventromesad to its insertion on the dorsal rim of the gonocoxopodite (fig. 30).

Muscles of the Clasping and Intromittent Organs

The following nine muscles of the male horsefly include the intrinsic muscles of the gonocoxopodites, muscles associated with the endophallic armature, and muscles of the aedeagus. Presumably they all belong to the ninth abdominal segment. The tergal and sternal muscles of the eighth and ninth abdominal segments (*176, 180* and *184*), which activate the gonocoxopodites as a whole, have been described above.

185. *Gonocoxal muscle of the aedeagal apodeme* (figs. 29 and 30). Originates posteriorly on the dorsal, proximal rim of the gonocoxopodite. The fibers extend anterad to their insertion on the aedeagal apodeme.

186. *Ventral intrinsic muscle of the gonocoxopodites* (figs. 27 and 29). A broad, apparently unpaired, band of muscle fibers originating on the ventral, proximal surface of the fused gonocoxopodites. The fibers run posterad and converge slightly to their in-

sertion on the "crotch" of the gonocoxopodites, near the base of the aedeagus.

187. *Adductor of the gonostylus* (fig. 30). A relatively large muscle originating on the lateral, proximal wall of the gonocoxopodite, tapers to its insertion by a short tendon on the mesal, proximal lip of the gonostylus.

188. *Abductor of the gonostylus* (fig. 30). Shorter and less robustly developed than the adductor muscle. Origin on the lateral wall of the gonocoxopodite, distal to the origin of *187*; tapers to its insertion on the lateral, proximal lip of the gonostylus.

189. *Median ventral muscle of the endophallic armature* (figs. 23 and 29). Origin on the anteroventral end of the endophallic apodeme; extends posterad to its insertion, by a short hyaline apodeme, to the "hilt" of the endophallic armature.

190. *Protractor of the endophallus* (fig. 29). Inserted anteriorly on the lateral surface of the endophallic apodeme; extends posterolaterad to its origin on the base of the aedeagus (fig. 30).

191. *Retractor of the endophallus* (figs. 29 and 30). Origin on the anterior end of the aedeagal apodeme, proceeds posteromesad to its insertion on the "hilt" of the endophallic armature.

192. *Accessory retractor of the endophallus* (fig. 30). Origin on the lateral surface of the endophallic apodeme, dorsal to the origin of *190*; passes posterad to its insertion on the lateral wall of the endophallus near the gonopore.

193. *Aedeagal muscle of the endophallic apodeme* (fig. 30). Origin on the anterior end of the aedeagal apodeme; insertion on the anterior end of the endophallic apodeme. When contracted, this muscle forms a short, fusiform bundle.

Muscles of the Proctiger

(Tenth and Eleventh Abdominal Segments)

194. *Dorsal longitudinal muscle* (fig. 26). Very small. Origin on the anterior margin of the tenth abdominal tergite of the female; inserted posteriorly on the base of the terminal lobe of the abdomen, *XI ?*, beneath the cercus. Absent in the male.

195. *Lateral oblique muscle of the proctiger* (fig. 27). Origin on the ventral plate of the proctiger; insertion on the base of the terminal lobe of the abdomen, *XI ?*, beneath the cercus. This anomalous muscle occurs only in the male.

196. *Dorsoventral muscle of the cercus* (figs. 26 and 27). A minute vertical muscle attached dorsally on the mesal margin of the cercus; attached ventrally on the ventral plate of the proctiger. Very similar in both sexes.

The Muscles of the Ventral Diaphragm

The ventral diaphragm of the abdomen is provided with numerous muscle fibers; these fibers are the ventral transverse muscles of the abdomen and are attached laterally to the upper portions of the sternal plates.

The Abdominal Mechanism

The skeleto-muscular system of the abdomen serves six important functions in the horsefly. Circulation of the blood is aided by contractions of the dorsal and ventral transverse muscles which produce pulsations of the dorsal and ventral diaphragms. The spiracular muscles regulate the opening and closing of the spiracles. Most of the muscles of the pregenital segments are involved in producing the breathing movements of the abdomen and are important in respiration. The movements of body parts involved in copulation, insemination, and oviposition are effected primarily by abdominal muscles inserted on cuticular parts. The following discussion deals with the last four abdominal functions.

Breathing Movements

When a horsefly rests after periods of activity, and during feeding, breathing movements can be observed in the abdomen: dorsoventral compression and shortening of the abdomen alternates with expansion and extension of the abdomen. The function of these breathing movements is to bring about a partial ventilation of the tracheal trunks. This incomplete renewal of air in the tracheal system of the horsefly is undoubtedly aided by the development of large tracheal sacs. Wigglesworth (1947), reviewing the work of other investigators on the breathing movements of insects, states that changes in pressure due to breathing movements are transmitted from the body wall by the blood; in regard to the tracheal sacs he believes that, " even where these lie in rigid parts such as the head or legs, the changes in pressure produced by the respira-

tory movements of the abdomen will be transmitted to them by the blood".

In terms of the skeleto-muscular system, the general explanation of the breathing movements of the abdomen of the horsefly is quite simple (text figure 1, *cf.* fig. 24). Shortening of the abdomen is accomplished by contractions of the median dorsal longitudinal muscles (*mdl*), the lateral dorsal longitudinal muscles (*ldl*), and the ventral longitudinal muscles (*vlm*) which retract the individual tergal and sternal plates. The dorsoventral and external lateral muscles (*dvm* and *elm*) compress the abdomen by drawing the tergal and sternal plates closer together. The external lateral muscles of each segment are apparently able to pull the tergal plate forward when the sternum is held stationary by the contraction of the ventral longitudinal muscles of the preceding segment. Extension and dilation of the abdomen are both brought about by contraction of the external dorsal and external ventral muscles (text figure 1, *edm* and *evm*). The external dorsal muscles are reversed and oblique; thus their attachments on the succeeding tergal plates are anterior to their attachments on the segment being considered. Contraction of the external dorsal muscles decreases the overlap between tergal plates and also pulls the tergal plates dorsad. The external ventral longitudinal muscles (*evm*) decrease the overlap between successive sternal plates and, because they are almost vertical and reversed, contraction of these muscles forces the sternal plates of each succeeding segment ventrad. Thus, most of the muscles of the pregenital segments play a part in producing breathing movements of the abdomen. Since the accessory and second accessory dorsal muscles (adm_1 and adm_2) are restricted to the posterior pregenital segments of the male, they probably do not play an important part in the respiratory movements; they are concerned with movements of the tip of the abdomen during copulation.

Copulation and Insemination

Although naturalists have been observing the habits of horseflies for many years, Bailey's (1948) review of the literature on hovering and mating of Tabanidae indicates that our knowledge of these subjects is meager and fragmentary. Furthermore, very few horseflies have been observed in coitus in the laboratory. Copulation of

Tabanus sulcifrons has been recorded in the field by Hine (1903); his account is as follows: " the day is clear and warm; *T. sulcifrons* abundant along the south side of the woods; between eight o'clock and half past eight several pairs observed copulating on the fence and several pairs taken. The male in every instance clung to the edge of a rail, and the female with the legs and wings motionless and touching nothing hung suspended ". None of the observations in the literature provide the investigator with the physical details or mechanism of copulation and insemination. Fortunately a good deal of information on the mechanics of these complicated processes can be obtained by dissection and micromanipulation of parts in preserved and fresh specimens.

The clasping apparatus of the male consists of the fused gonocoxopodites and the movable gonostyli (figs. 22 and 30). The clasping apparatus as a whole may be partially rotated by alternate contractions of the anterior tergal muscles of the gonocoxopodite (figs. 27 and 29, *176*); on the other hand, the posterior end of the clasping apparatus is tilted ventrad when these muscles contract together. The posterior tergal muscles of the gonocoxopodites (figs. 27 and 30, *184*) are also rotators of the clasping apparatus and may, by their simultaneous contraction, elevate the entire clasping apparatus. The sternal retractors of the gonocoxopodites (figs. 27 and 29, *180*) have the primary function of anchoring the external genitalia during the process of coition. Very little is known of the positions assumed by the males and females during the initial stages of copulation; therefore the exact sequence of events cannot be discussed in terms of the skeleto-muscular system. In the final position of copulation the horseflies are attached end to end and face in opposite directions. The male grasps the female with the movable gonostyli which are activated by adductor and abductor muscles (fig. 30, *187* and *188*). The female is held by adduction of the gonostyli and is released when the gonostyli are abducted; the adductor muscles are much more powerfully developed than the abductors.

The aedeagus is the intromittent organ; it is fixed, rigid, and tapers posteriorly. The aedeagus cannot be distended or erected by blood pressure or any other mechanism, and is merely inserted into the genital chamber of the female during the clasping process. The ejaculatory duct does not extend into the aedeagus but empties

into a thin walled tube, the *endophallus*, (figs. 22, 23, and 30), which opens at the apex of the aedeagus. Associated with the endophallus is a complex armature; this armature has been described on page 161. The endophallus, the endophallic armature, and the endophallic muscles constitute a complex mechanism for transferring the sperm from the male gonopore to the genital chamber of the female. Although ejaculation has never been witnessed in a living specimen, dissections indicate that insemination is brought about in the following manner:

The transfer of sperm from the male to the female is accomplished largely by protractive and retractive movements of the endophallic armature (fig. 23a and b). The sperm leaves the ejaculatory duct by way of the gonopore and enters the endophallus. When the endophallic armature is protracted (fig. 23b), that portion of the endophallus anterior to the endophallic guard is longitudinally collapsed, and the apices of the endophallic tines and guide are pushed through the posterior opening (phallotreme) of the aedeagus. The endophallic tines and guide prevent dorsoventral collapse of the endophallus. It is important to note that the endophallus is not everted when the endophallic armature is protracted.[6] Thus the endophallus is provided with a pushing apparatus that apparently moves the male sexual products through the aedeagus. It seems that the sperm would have to be in the form of packets in order for this mechanism to be effective. Unfortunately, the author has never been able to find sperm in the endophallus of the horseflies dissected. Nevertheless, there can be no doubt that the sperm in one form or the other must pass through the endophallus and that protraction and retraction of the endophallic armature is operative during the process of insemination.

Manipulations on fresh and fixed specimens demonstrate that the endophallic armature is pulled posterad (fig. 23b) by the contraction of the protractors of the endophallus (figs. 29 and 30, *190*). The endophallic armature is pulled anterad by the retractors of the endophallus (figs. 29 and 30, *191*). The aedeagal muscles of the endophallic apodeme (fig. 30, *193*) serve as additional retractors

[6] The walls of the endophallus are fixed to the endophallic guard, which in turn, is immovably attached to the walls of the aedeagus; for this reason, the endophallic armature can be protracted only partially and the endophallus is prevented from being turned inside out.

of the endophallus. The accessory retractors of the endophallus (fig. 30, *192*) originate on the endophallic apodeme and are inserted on the lateral walls of the endophallus; this paired muscle differs from the preceding retractor muscles in that it acts directly on the endophallus rather than on the endophallic armature. Contraction of the gonocoxal muscle of the aedeagal apodeme (fig. 30, *185*) steadies the slender aedeagal apodeme and provides a firmer origin for the protractor and retractor muscles attached there. Thus, most of the muscles of the endophallic apparatus are either protractive or retractive in function. However, two muscles remain which are very difficult to interpret. The median ventral muscle of the endophallic armature (figs. 23 and 29, *189*) is an unpaired muscle that seems to have its anterior and posterior attachments on fixed points. Micromanipulations indicate that the endophallic apodeme may be arched slightly (fig. 23b); the author believes that this muscle has a jarring action on the endophallic armature which probably aids in the deposition of the sperm or sperm packets. The function of the ventral intrinsic muscle of the gonocoxopodites (fig. 29, *186*) could not be determined.

Oviposition

The act of oviposition in the horsefly has not been minutely studied by field observers. The accounts published by Hine (1903) for *Chrysops callidus* and by Cameron (1930) for *Haematopota pluvialis* are essentially in agreement: at the time of egg laying, the head of the female is lowered and the abdomen is bent ventrad and anterad. After each egg is deposited, the pseudovipositor consisting of the genital and postgenital segments is withdrawn and the abdomen is straightened. Cameron states, "each egg as it is laid, receives a thin coating of cement, which is brushed on by the tip of the ovipositor".

The ventral and anterior bending of the abdomen, while depositing an individual egg, is accomplished primarily by contraction of the ventral longitudinal muscles (fig. 24, *119, 126, 135,* etc.), the external dorsal muscles (*117, 124, 132,* etc.) and the external ventral muscles (*120, 127, 136,* etc.). Contraction of the series of ventral longitudinal muscles increases the overlap of sternal plates, and contraction of the external dorsal muscles decreases the overlap of tergal plates; consequently, the exposed tergal area of the

abdomen is longitudinally increased and the exposed sternal area is longitudinally decreased. Contraction of the external ventral muscles of each segment depresses the sternal plate on the hinge formed by the ventral longitudinal muscles (fig. 24). These unequal adjustments of the dorsal and ventral segmental plates cause the end of the abdomen to become recurved. The genital and postgenital segments, which are telescoped into the seventh abdominal segment (fig. 26), are not provided with external dorsal and external ventral muscles. These segments may be protracted by compression of the abdomen by the contraction of the dorsoventral muscles, particularly those of the fifth through seventh abdominal segments. During the interval between the deposition of one egg and the laying of another, the abdomen is straightened and the genital and postgenital segments are withdrawn. This is undoubtedly accomplished by relaxation of the external dorsal and external ventral muscles and by increasing the degree of overlap of the tergal plates by contraction of the median and lateral dorsal longitudinal muscles (fig. 24). The genital and postgenital segments are re-telescoped by contractions of the median and lateral dorsal longitudinal muscles of the seventh abdominal segment (fig. 26, *100* and *101*), the ventral longitudinal muscle of the seventh segment (*100*), the median and lateral dorsal longitudinal muscles of the eighth abdominal segment (*172* and *173*), the retractor of the genital chamber (*181*), and the dorsal longitudinal muscles of the ninth and tenth abdominal segments (*182* and *194*).

The muscles of the oviducts and the genital chamber control the passage of eggs from the time they issue from the ovarioles until they are finally deposited. The walls of the median and lateral oviducts are provided with circular and longitudinal muscle fibers; they are also activated by muscles originating on the seventh sternum. The oviduct is drawn anterad by contraction of the retractor muscles of the oviduct (fig. 26, *168*) and posterad by the protractor muscle (*167*). When protracted, the median oviduct is thrown into a series of folds. The posterior end of the median oviduct may be shut off from the genital chamber by the constrictors of the oviduct (*168*).

The genital chamber is capable of great mobility; it may be protracted, retracted, dilated and depressed by muscles of the eighth

and ninth abdominal segments (figs. 26 and 31). The tergal and sternal protractors of the genital chamber belong to the eighth abdominal segment (*177* and *178* respectively). The retractor of the genital chamber (*181*) is antagonistic to the two preceding sets of muscles and originates on the eighth abdominal sternum. The retractor-depressor of the genital chamber (*179*) functions to pull the chamber posterad as well as to depress its roof. The genital chamber is dilated by the modified dorsoventral muscles of the ninth abdominal segment (*183*); specifically, these muscles elevate the roof of the genital chamber which represents the venter of the ninth segment.

Summary

1. The cuticular parts of the head of the horsefly have been reviewed. The first sucking pump of the head is believed to be the modified cibarium. The author also agrees with Snodgrass (1935) in interpreting the sclerite of the lower part of the face as the clypeus, rather than the frontoclypeus as most authors have done. The maxilla of the male horsefly differs considerably from that of the female: the cardo of the male is lost, and the stipes is reduced to form a small lever. The cardo and stipes of the male have not fused with the hypostomal bridge as stated by some authors. The distal end of the labium is provided with six important sclerites; most of the intrinsic muscles of the labium are inserted on these sclerites. The pseudotracheal apparatus has been described and the apertures of the collecting channels have been located. The blood sucking apparatus consists of the cibarial pump and the pharyngeal pump. The esophagus is provided with a musculated valve which contributes greatly to the efficiency of the pharyngeal pump.

2. The origins, insertions, and functions of all of the muscles of the head and mouthparts of both sexes of the horsefly have been presented in this paper. The skeleto-muscular mechanism of feeding has been discussed in detail on pages 149-154. The functions of most of the muscles have been established by dissection and micromanipulation of preserved and freshly killed specimens.

3. There are 54 muscles in the head of the female and 46 muscles in the head of the male. All of the muscles in the head of the male can be homologized with muscles in the female, although

some of the muscles of the former have become modified. The muscle pattern of the head of the male can be derived from the ground plan of the female by mere subtraction.

4. The abdominal musculature of both sexes has proved invaluable in establishing the homologies of cuticular parts of the abdomen. This does *not* mean that all of the abdominal muscles can be used for interpreting the skeletal structure of the abdomen. Only those muscles which are serially repeated and are constant in their origins and insertions were considered reliable.

5. Ten segments are clearly indicated by the arrangement of serial muscles in the abdomen of both sexes, and the presence of an eleventh abdominal segment is strongly suggested by the muscles in the proctiger. The clasping organs of the male are believed to be true gonopods of the ninth abdominal segment. The gonostyli are activated by muscles originating in the gonocoxopodites. The genital chamber of the female, which receives the intromittent organ of the male during copulation, is formed by invagination of the body wall directly behind the eighth abdominal sternum. The roof of the genital chamber is formed by the venter of the ninth abdominal segment and the lateral sclerites of the roof of the genital chamber are sternites of the ninth segment. Organs of oviposition, derived from segmental abdominal appendages, are entirely lacking in the female horsefly.

6. The penis and the penis valves have fused in the horsefly to form the complex intromittent organ known as the aedeagus. The aedeagus cannot be erected or distended. The ejaculatory duct empties into a thin walled tube; this tube is the endophallus which lies within the aedeagus. The endophallus is provided with an elaborate armature which is described on page 161. Nine muscles are directly associated with the endophallic armature. Insemination of the female is brought about primarily by protractive and retractive movements of the endophallic armature.

7. There are 141 muscles in the abdomen of the female and 154 in the male. A basic plan of musculature pervades the abdominal segments of both sexes of the horsefly. This basic plan is followed rather closely in the pregenital segments and is greatly modified but still recognizable in the genital and postgenital segments.

8. The skeleto-muscular mechanisms of the horsefly that bring about the abdominal breathing movements and the movements of body parts during copulation, insemination, and oviposition have been discussed for the first time in this paper.

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EXPLANATION OF FIGURES

In the plates which follow, labels are printed in their entirety, eliminating the need for a table of abbreviations. In a few cases abbreviated labels were necessary; these abbreviations are explained in the explanation of figures in which they occur. Muscles are indicated on the plates by numbers. The reader is referred to the appropriate section of the text in which the particular muscle is numbered and described.

Fig. 1.—Anteroventral aspect of head of female *T. sulcifrons* (M, median suture of frons; GR, vertical groove of clypeus; T, proximal sclerite of labrum). Fig. 2.—Same as preceding. Male *T. sulcifrons.*

Fig. 3.—Posterior view of head of female *T. sulcifrons* (X, suture of stipes). Fig. 4.—Same view of head of male *T. sulcifrons.*

Fig. 5.—Parasagittal section of head of female *T. sulcifrons* showing endoskeleton (P, plate between dorsal and anterior tentorial arms; PT, process of tentorium).

Fig. 6.—Lateral view of labium (A, articulatory process of theca; B, distal sclerite of labial stalk; C, posterior labellar sclerite; C′, process of posterior labellar sclerite; D, lateral labellar sclerite).

Fig. 7.—A. Apex of mandible of *T. sulcifrons* with minute teeth on mesal edge. B. Apex of galea of female *T. sulcifrons.*

Fig. 8.—Cross section of the mouthparts of female *T. sulcifrons,* cut near the middle of the labial stalk.

Fig. 9.—A microphotograph of the ventral surface of the dissected pseudotracheal membrane of female *T. sulcifrons* (AACC, aperture of anterior collecting channel; ACC, anterior collecting channel; APCC, aperture of posterior collecting channel; IP, independent pseudotracheae; IS, interlabellar sclerite; PCC, posterior collecting channel; PST, pseudotracheae).

Fig. 10.—Parasagittal section of head of female *T. americanus,* cut to the left of the midline; general view of muscles of sucking pumps and

labium (B, distal sclerite of labial stalk; D, lateral labellar sclerite; MP, median process of labrum).

Fig. 11.—Cross section of head of female *T. americanus*, sucking pumps and left mandible removed; general view of muscles of mouthparts (ML, leverlike, mesal process of maxilla).

Fig. 12.—Parasagittal section of head of male *T. sulcifrons*, cut to left of midline. Fig. 13.—Lateral view of right antenna of male *T. sulcifrons*.

Fig. 14.—Lateral views of right maxillae and maxillary muscles of female and male *T. sulcifrons*. A. Female maxilla retracted; B. Female maxilla protracted; C. Male maxilla retracted; D. Male maxilla protracted.

Fig. 15.—Passage of blood through sucking pumps of female *T. sulcifrons* (indicated by arrows). A. Blood in cibarial pump (MP, median process of labrum); B. Blood in pharyngeal pump; C. Blood in esophagus. The mandibles which form the posterior wall of the food canal have been removed.

Fig. 16.—Lateral view of abdomen (pregenital segments) of *T. sulcifrons*. Fig. 17.—Dorsal view of posterior end of abdomen of male, genital and postgenital segments pulled out. Fig. 18.—Lateral view of posterior end of female abdomen. Fig. 19.—Lateral view of posterior end of male abdomen. Fig 20.—Dorsal view of posterior end of female abdomen. Fig. 21.—Ventral view of posterior end of female abdomen.

Fig. 22.—Ventral view of external genitalia and postgenital area of male *T. sulcifrons*. Fig. 23.—Parasagittal section of the aedeagus of *T. sulcifrons*; general view of endophallus and endophallic armature. A. Endophallic armature retracted; B. Endophallic armature protracted.

Fig. 24.—Sagittal section of abdomen of female *T. sulcifrons* showing muscles of pregenital area.

Fig. 25.—Muscles of fifth and sixth abdominal segments of male *T. sulcifrons*.

Fig. 26.—Longitudinal section of posterior end of abdomen of *T. sulcifrons* showing muscles and genital invaginations of female.

Fig. 27.—Same view as preceding of male.

Fig. 28.—Dorsal view of the female reproductive tract of *T. sulcifrons* showing muscles of genital chamber; left accessory gland removed, ovarioles immature.

Fig. 29.—Ventral view of male genital system of *T. sulcifrons* showing muscles associated with external genital organs. Fig. 30.—Dorsal view of male reproductive system; internal reproductive organs displaced. Muscles of clasping and intromittent organs numbered. Fig. 31.—Dorsal view of subgenital plate (sternum VIII) of female showing muscle attachments.

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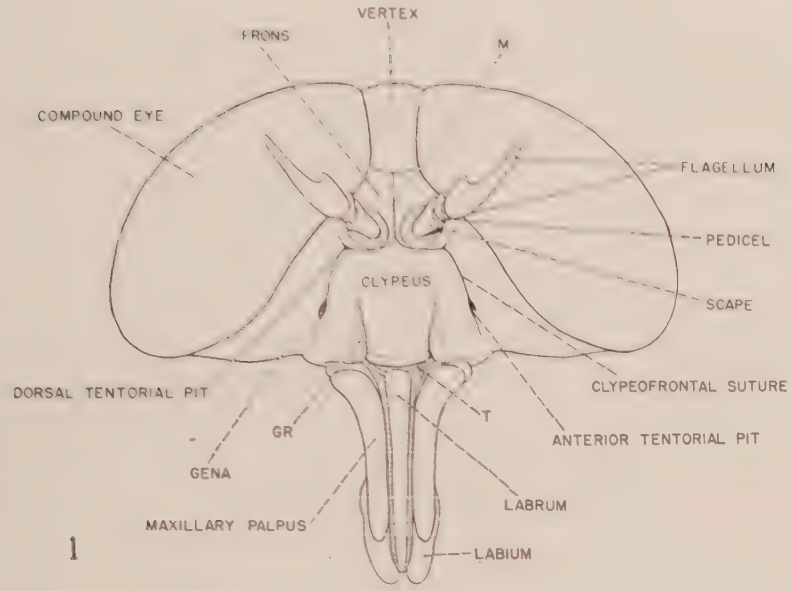

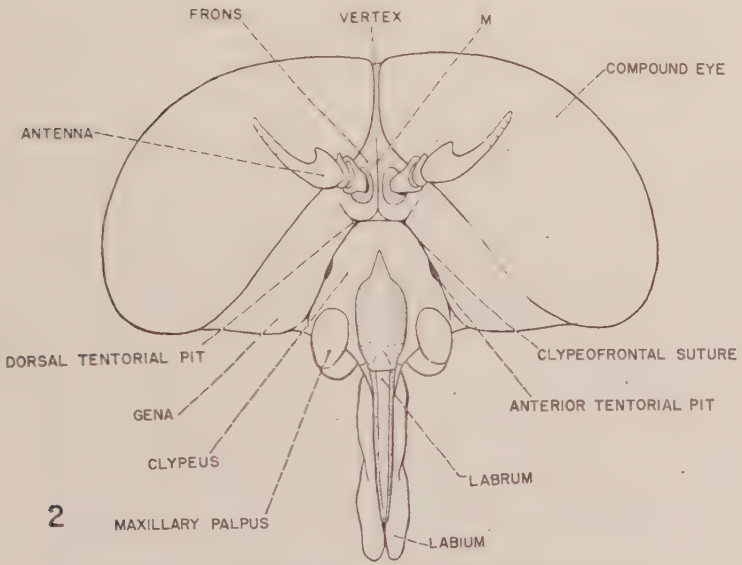

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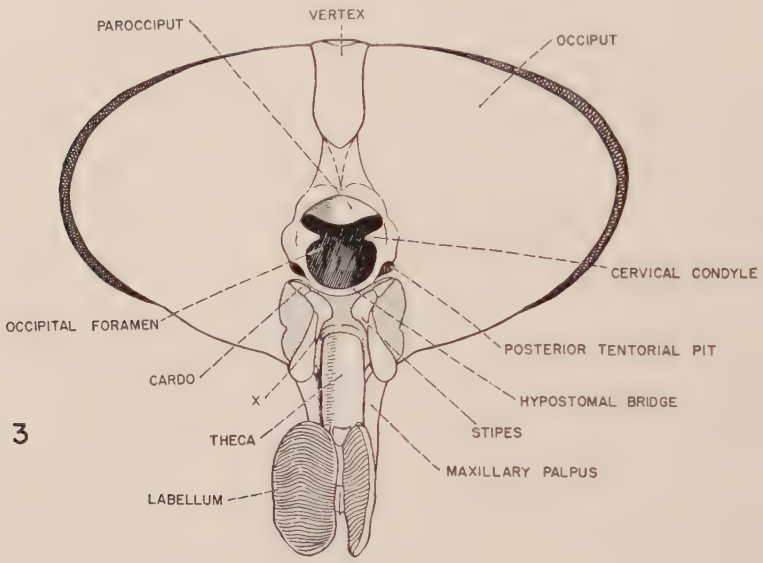

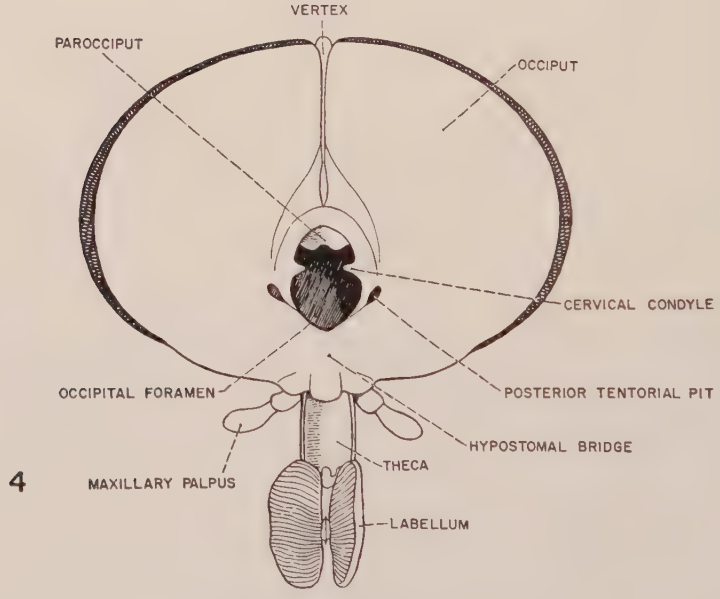

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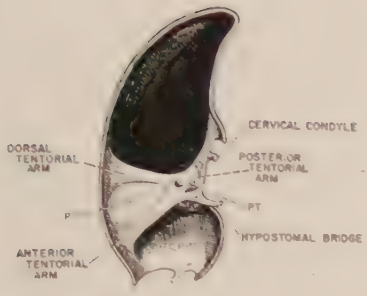

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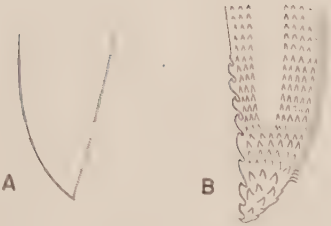

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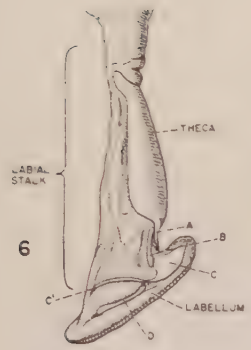

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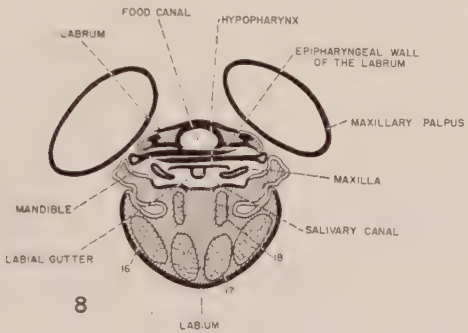

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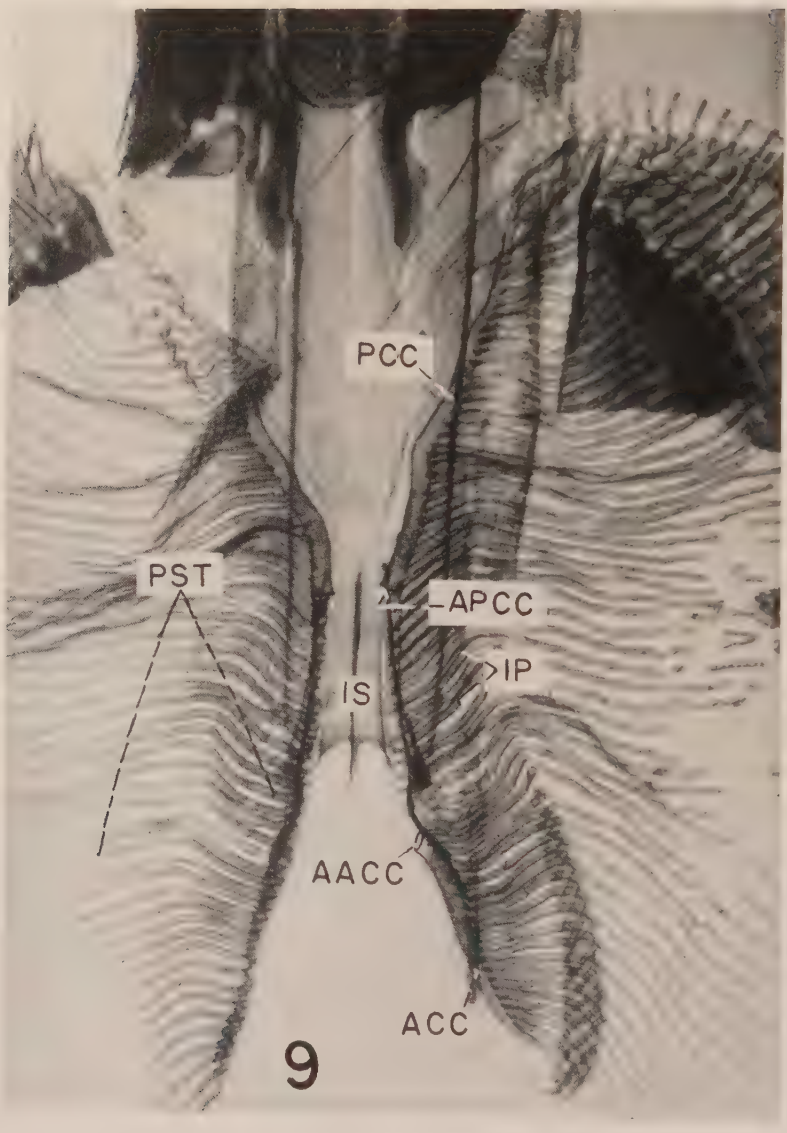

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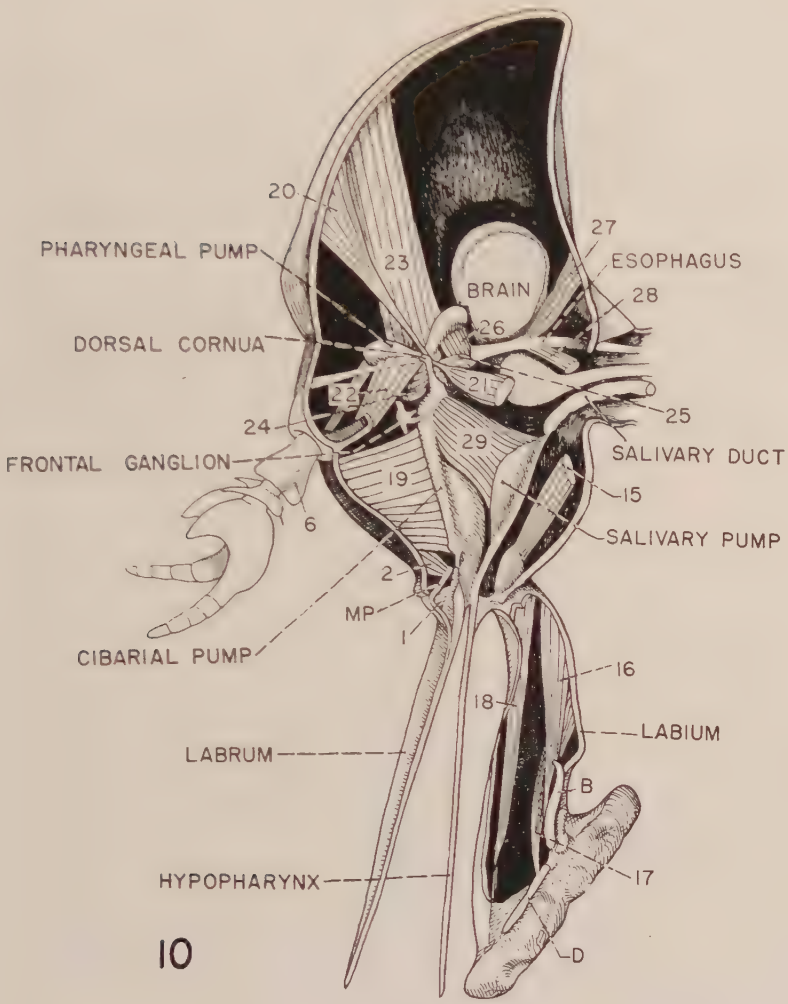

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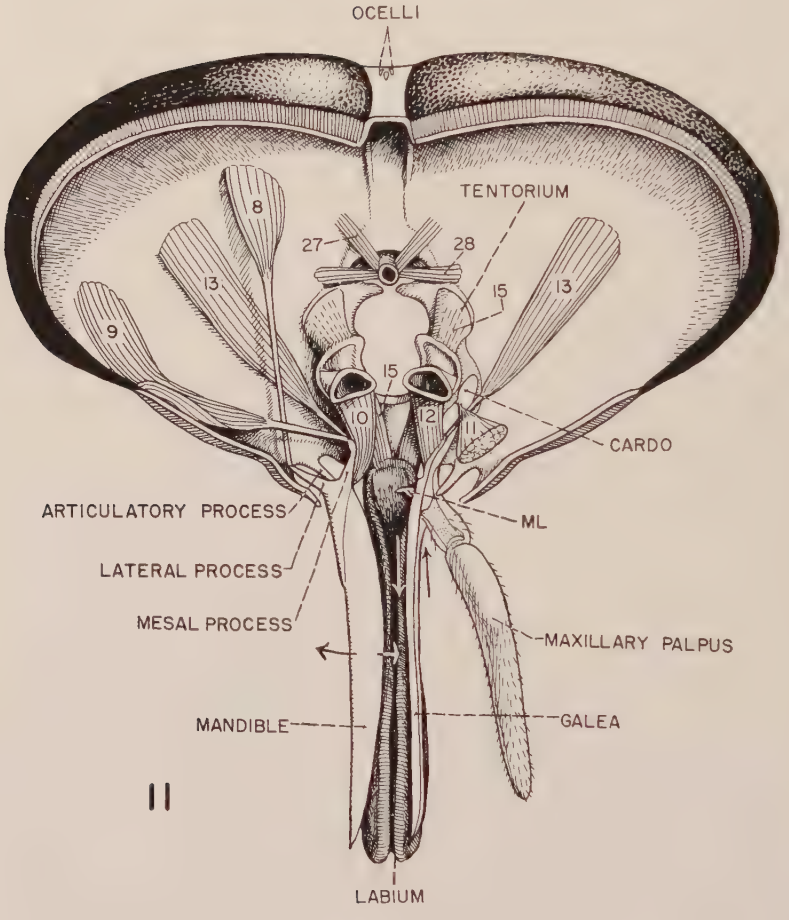

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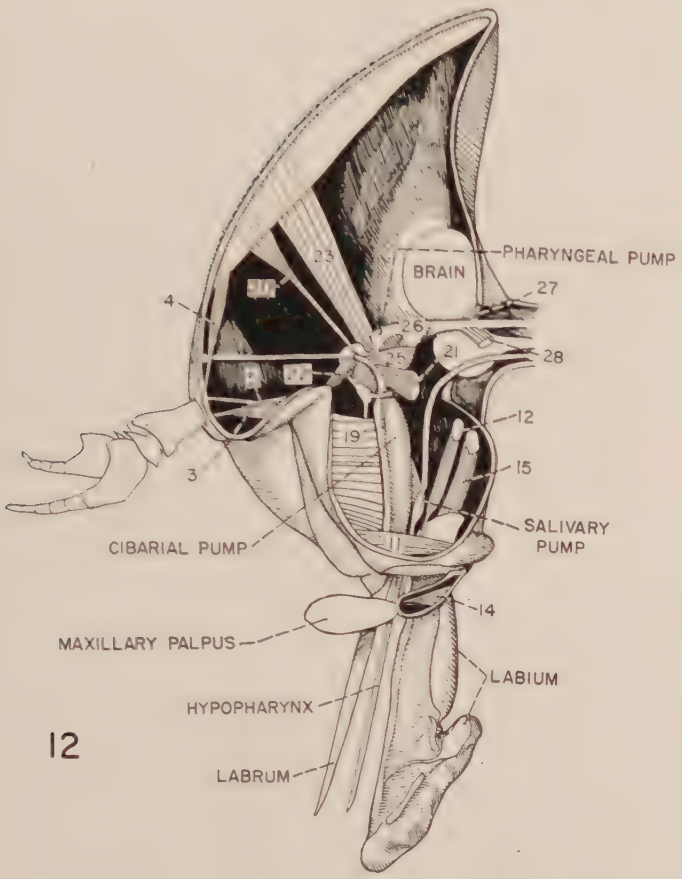

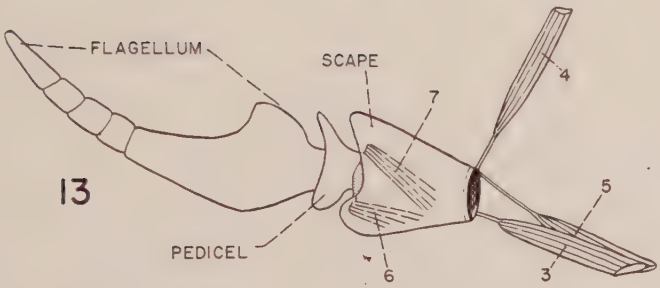

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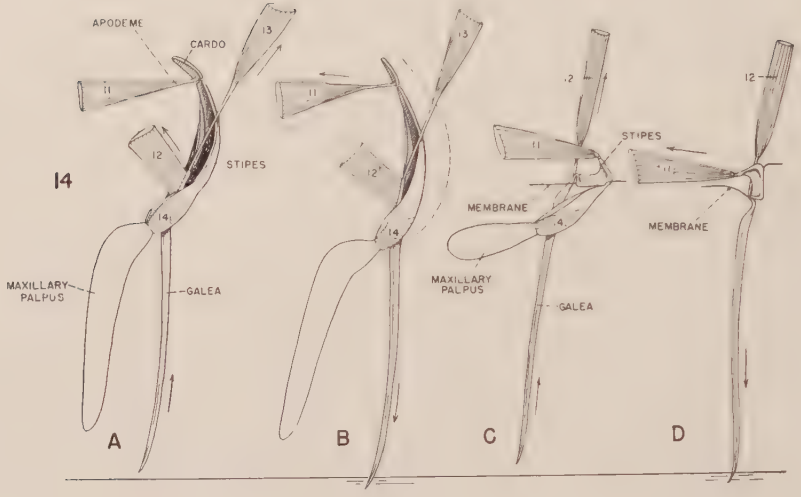

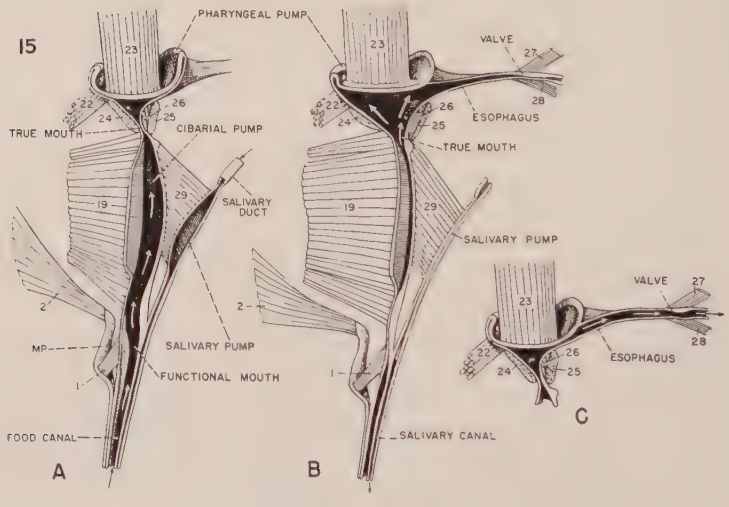

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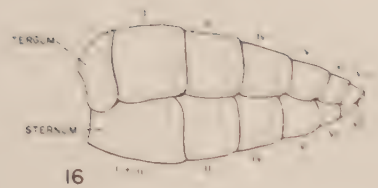

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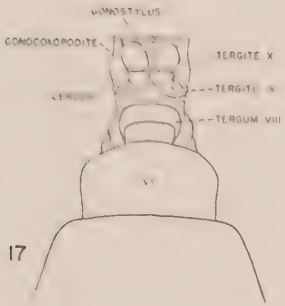

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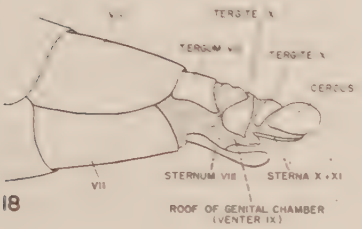

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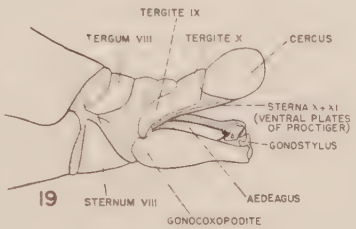

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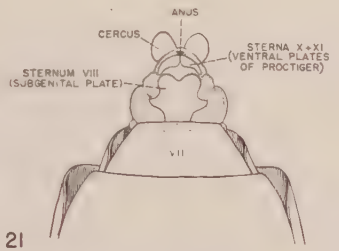

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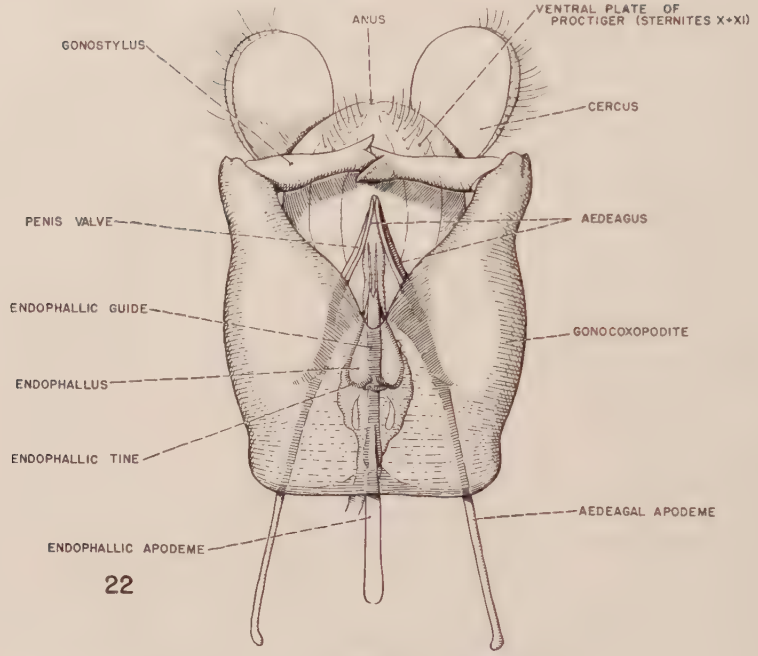

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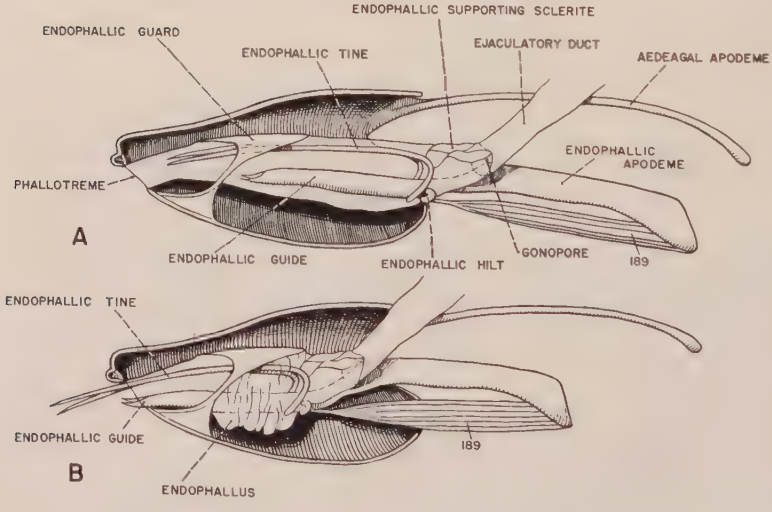

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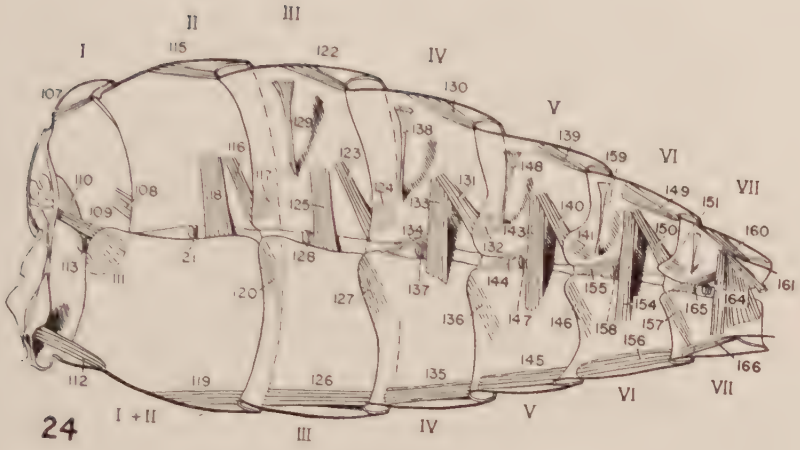

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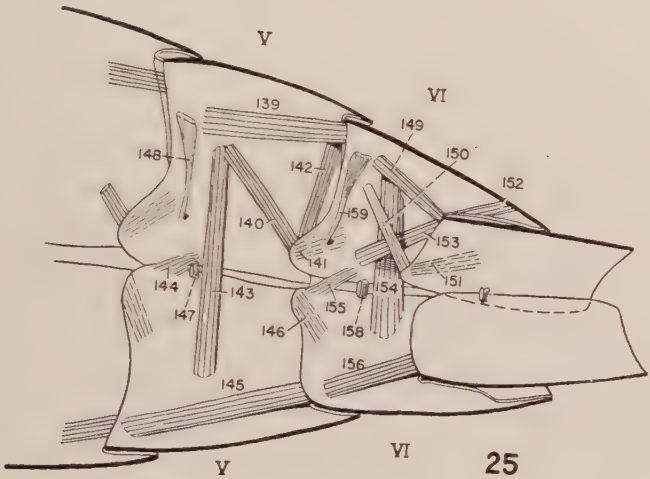

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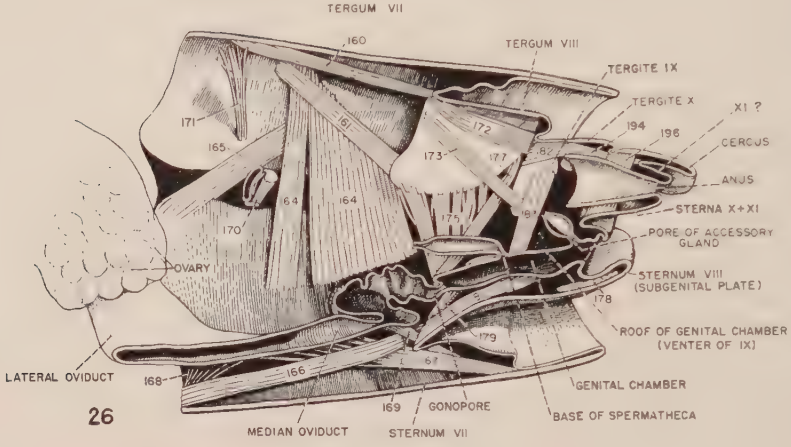

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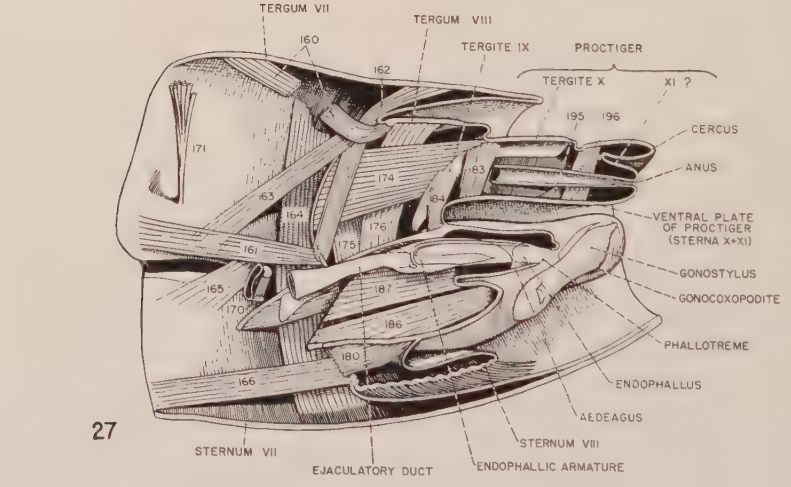

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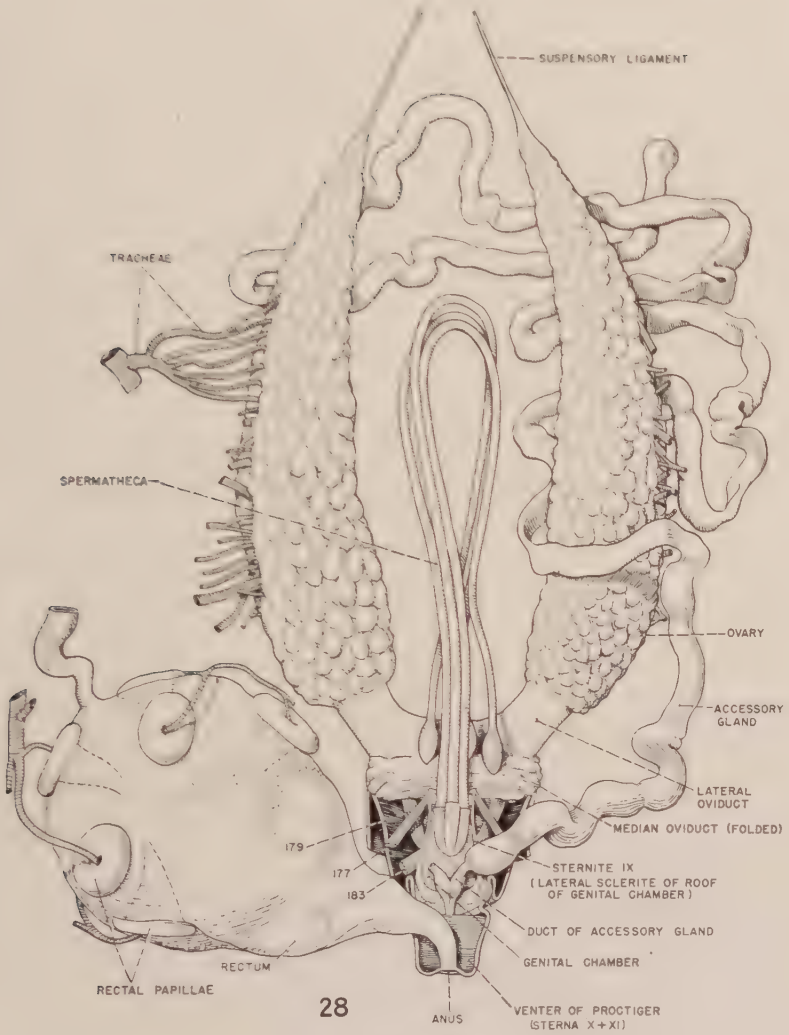

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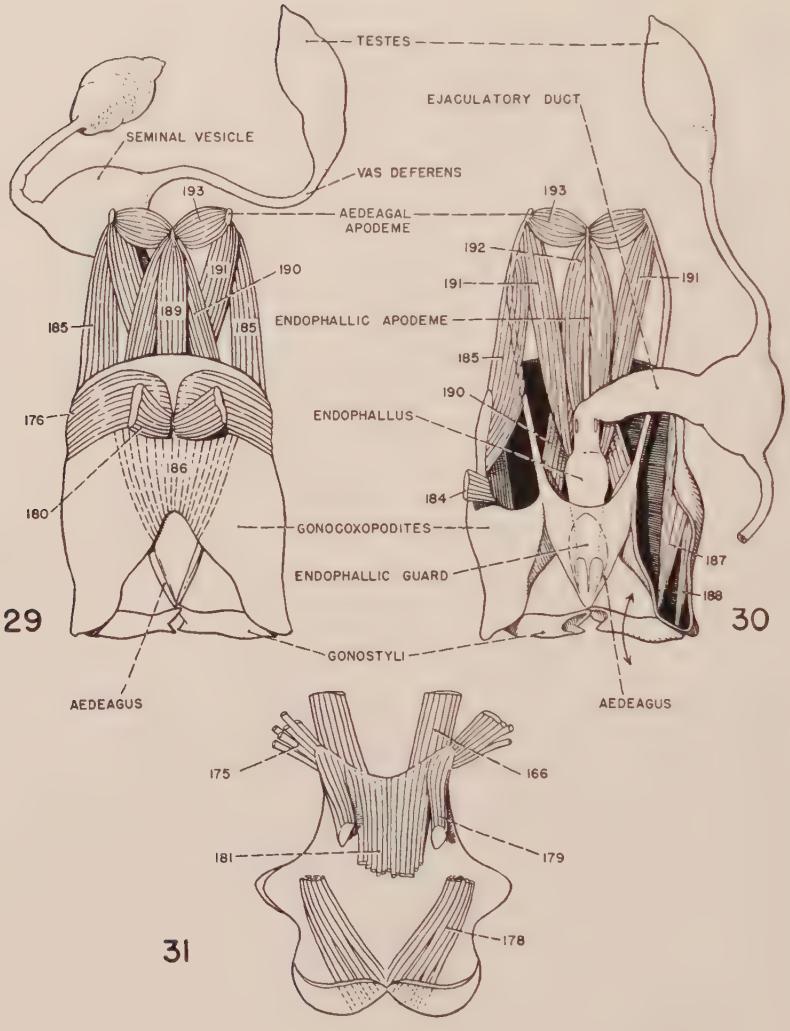

BONHAG—SKELETO-MUSCULAR MECHANISM

A TAXONOMIC STUDY OF THE NEARCTIC SPIDER WASPS BELONGING TO THE TRIBE POMPILINI (HYMENOPTERA: POMPILIDAE). PART III

BY HOWARD E. EVANS

Kansas State College, Manhattan, Kansas

(Plates VI to XV)

In two earlier papers under this same title,[1] I have presented an introduction to the study of the Nearctic Pompilini and a systematic treatment of nine of the thirteen genera. In this, the final part, the remaining four genera (*Pompilus*, *Aporinellus*, *Allochares*, and *Paracyphononyx*) are treated. Following this, I have appended a number of supplementary sections. First, I have presented a short list of species which cannot be recognized, and which are therefore otherwise omitted from this work. Following this is a section entitled "Addenda", in which I have brought together certain additional information which has become available regarding the genera and species covered in Parts I and II. The concluding portion of the text is in the form of a general summary, in which I have attempted to analyze the composition of the Nearctic fauna and to make certain suggestions regarding the possible phylogeny of the Nearctic genera. A check list and an index covering all three parts are included at the end.

X. Genus **POMPILUS** Fabricius[2]

Pompilus Fabricius, 1798, Suppl. Ent. Syst., pp. 212, 246-252. [Type: ***Pompilus pulcher*** Fabricius, 1798; fixed by Opinion 166 of the Internat. Comm. Zool. Nomen., issued Aug. 1945.]—Latreille, 1802, Hist. Nat. Crust. Insect., III, pp. 334-335.—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 86. [In part.]—Cresson, 1887, Synopsis Hymen., Suppl. Vol. Trans. Amer. Ent. Soc., pp. 110, 270-271. [In part.]—Berland, 1925, Faune de

[1] Evans, H. E., 1950, Trans. Amer. Ent. Soc., 75: 133-270. (Part I.)
Evans, H. E., 1951, Trans. Amer. Ent. Soc., 76: 207-361. (Part II.)

[2] For full synonymy, see also the several subgenera.

France X, Hymen. vespiformes I, pp. 257-273.—Richards, 1937, Gen. Names Brit. Insects, pt. 5, p. 126.—Wilcke, 1942, Ent. Berichten, 11: 23-25.—Wilcke, 1943, Overdr. Med. Landbouwhoogeschool Wageningen, 47: 46.—Evans, 1950, Trans. Amer. Ent. Soc., 75: 150.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 933.

Psammochares Sustera, 1913, Verh. zool.-bot. Ges. Wien, 62: 210. [Type: *Sphex plumbea* Fabricius, 1787.] [*Nec* Latreille, 1796.]—Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, pp. 150-151. [In part.]—Arnold, 1937, Ann. Transvaal Mus., 19: 43.

Aporoideus Banks, 1941, Proc. Acad. Nat. Sci. Phila., 92: 353. [*Nec* Ashmead, 1902.]

The generic name *Pompilus* has never been used in exactly the same sense as used by the present author. Previous authors have been inclined to use it as a blanket genus to include a variety of unspecialized Pompilini (for example, Berland, 1925, and many of the early authors), or in a very restricted sense to include only the genotype and perhaps a few other species (for example, Wilcke, 1943). In the present treatment I have effected something of a compromise between these two extremes. *Agenioideus, Sericopompilus, Anoplius,* and *Evagetes,* though closely related, seem to me to constitute discrete genera, which have already been treated as such. On the other hand, Wilcke's *Ammosphex,* Banks' *Anoplochares,* and several other groups, do not appear to me to be sufficiently discrete to be considered full genera, and they are here treated as subgenera of *Pompilus.* In all, six subgenera are recognized in North America, and a seventh, *Pompilus s. str.,* is treated briefly, although it does not occur in the New World.

The genus *Pompilus* is more noteworthy for the absence of any distinguishing characteristics than otherwise. The genus is a rather generalized one, derived possibly from *Agenioideus,* with which it seems to be linked via the subgenus *Hesperopompilus.* The pulvillar comb is for the most part more strongly developed than in *Agenioideus,* and the venation of a more advanced type, i.e., the veins and cells extend less close to the wing margin, the second recurrent vein arising halfway or less of the distance from the base of the subdiscoidal vein to the wing margin. Many of the other genera of Pompilini are essentially variations on the *Pompilus* theme and possibly derived from this genus or its ancestral stock.

Generic characters.—Small to fairly large wasps, 4 to 20 mm. in length. Ground color black, the abdomen sometimes marked with rufous, the legs occasionally so. Pygidium of female with or without setae, never with stout bristles. Mandibles of male unidentate, of female unidentate or bidentate. Malar space short or practically absent. Front flat or convex, never tuberculate; eyes in the female subparallel within or somewhat convergent above, the upper interocular distance at least .7 the lower interocular. Antennae slender, long or of moderate length, segment 3 in the female at least three times as long as its greatest thickness, segment 3 in the male usually but not always more than twice as long as thick.

Pronotum dorsally not longer than the mesonotum, usually much shorter, its posterior margin arcuate or angulate. Postnotum a transverse band of variable breadth, never strongly expanded on each side of the median line. Propodeum evenly sloping or with a more or less well-defined oblique posterior declivity, never tuberculate or rugose. Female with or without a tarsal comb. Claws of the female dentate, those of the middle and hind tarsi of the male dentate, those of the front tarsi of the male either dentate or bifid. Apical tarsal segments with or without spines beneath. Pulvillar comb variously developed, rarely as strong as in *Anoplius*, rarely as weakly developed as in *Agenioideus*. Cubitus of hind wing arising at or more often beyond the tip of the submedian cell. Transverse median vein of the fore wing interstitial or not with the basal. Stigma small or of moderate size; marginal cell of very variable length, the radial vein arcuate or sometimes angled at the third transverse cubital vein. Usually with three submarginal cells, but a few species with only two, in which case the second receives both recurrent veins. Second recurrent vein arising on the subdiscoidal vein halfway or less of the distance from the base of the subdiscoidal to the wing margin, the latter vein not reaching the wing margin.

Abdomen of female rather stout, subfusiform, the apex not noticeably compressed, the pygidium without bristles. Abdomen of male much more slender; sixth sternite with a median apical emargination of variable depth. Male genitalia variously developed; basal hooklets double, single, or wanting; parameres usually strong, more or less setose. The genitalia for the most part exhibit excellent subgeneric and specific characters.

Biology.—The species of *Pompilus* are spider-hunters of a rather generalized sort, usually not highly selective of their prey, but probably most often taking Lycosidae. The nest is constructed in sand or soft earth, except in one non-fossorial subgenus, *Anoplochares*. The biology is further discussed under the various subgenera and species. Except in the subgenus *Arachnospila*, very little is known of the biology of the North American forms.

Distribution.—Cosmopolitan. The Nearctic forms can be placed in six more or less well-defined subgenera, separated in the following key. The subgenus *Pompilus s. str.* is also included in the

key, although it does not occur in our fauna. Certain other exotic subgenera are not included.

Key to Subgenera

Females

1. Apical tarsal segment without a median row of spines beneath which are about the same size as those on the preceding tarsal segments, either without spines beneath, or with not more than three near the base, the apical half bare, or with a complete row of very minute spines; posterior pronotal margin varying from broadly angulate to arcuate 2

   Apical tarsal segment with several median spines in a row beneath, which are about the same size as those on the preceding segments, and which form a row that extends at least beyond the middle of the segment; posterior pronotal margin with a distinct angulation 5

2. Front basitarsus with two comb-spines, one at the middle and one at the apex of the segment; third submarginal cell only a small fraction of the size of the second, or actually absent; front microscopically granulo-punctate, dull .....D. **Perissopompilus** new subgenus

   Front basitarsus with three (rarely four) comb-spines; third submarginal cell well developed, at least half as large as the second; front microscopically reticulo-punctate, somewhat shining 3

3. Apical tarsal segment with a complete row of extremely minute spines beneath; front basitarsus with three long comb-spines on the outer side, and two almost equally strong spines on the inner side, one at the apex; pulvillar comb strong, the setae rather stout ....A. **Pompilus** Fabricius

   Apical tarsal segment either without median spines beneath, or with 1 to 3 spines near the base, with apical half bare; front basitarsus with three long comb-spines, but without other spines on this segment rivalling these in length 4

4. Apical tarsal segment without spines beneath; propodeum and mesopleura bare or with dark hairs; pulvillar comb weakly developed.
   B. **Hesperopompilus** Evans

   Apical tarsal segment with from 1 to 3 spines near the base; propodeum and mesopleura, as well as the temples, propleura, and front coxae, with abundant white hair; pulvillar comb strong, of at least 20 setulae.
   C. **Xerochares** new subgenus

5. Tarsal comb absent; anterior margin of clypeus slightly, evenly concave, the labrum exserted beyond the clypeus to about half the length of the latter .....G. **Anoplochares** Banks

   Tarsal comb present, the spines of variable length; labrum but slightly if at all visible beyond the apical margin of the clypeus 6

6. Marginal cell of the fore wing 1.3 or more times its own length from the tip of the wing (Figs. 239 and 240); front at most moderately hairy.
   E. **Ammosphex** Wilcke

Marginal cell of the fore wing approximately its own length from the wing-tip (Fig. 241); front, in fact most of the head, thorax, and propodeum, with a considerable amount of erect hair.

F. **Arachnospila** Kincaid

Males

1. Apical segment of front tarsus nearly parallel-sided, the inner margin not at all produced (Figs. 226-228); posterior pronotal margin arcuate or broadly subangulate; either the basal hooklets of the genitalia single or absent, or the sixth sternite with a flat median area set off by a carina ..2

   Apical segment of front tarsus shorter and wider, with a distinct expansion on the inner margin, therefore asymmetrical (Figs. 229 and 230); posterior pronotal margin usually distinctly angulate; basal hooklets of genitalia double; sternite 6 unmodified 5

2. Both front tarsal claws bifid (Fig. 228); propodeum and mesopleura with abundant white erect hairs; head very thin; subgenital plate without basal palpus-like structures; sternite 6 unmodified.

   C. **Xerochares** new subgenus

   Outer front tarsal claw with the inner ray very short, therefore not or scarcely bifid (Figs. 226 and 227); propodeum and mesopleura without erect hairs or with a few dark hairs; either the subgenital plate with basal palpus-like appendages, or the sixth sternite with a flat median area set off by a carina 3

3. First four abdominal tergites with broad, complete transverse apical bands of very heavy silvery pubescence which diverges strongly from the median line; sixth abdominal sternite with a specialized, flattened median area set off by a carina (Fig. 178); basal hooklets of genitalia double (Fig. 177) .....D. **Perissopompilus** new subgenus

   Abdominal tergites without complete apical bands of heavy pubescence which diverge from the median line, though sometimes with a partial band of pubescence which is directed backward; sixth sternite not modified as above; basal hooklets single or wanting 4

4. Both claws of the front tarsus toothed, and weakly so (Fig. 226); apical margin of clypeus truncate; pulvillar comb fairly well developed.

   A. **Pompilus** Fabricius

   Inner claw of front tarsus bifid (Fig. 227); apical margin of clypeus rounded; pulvillar comb very weak. B. **Hesperopompilus** Evans

5. Last segment of front tarsus strongly lobed on the inner margin, the segment widest about mid-way; inner ray of inner claw of front tarsus short, rounded (Fig. 229); aedoeagus provided with a number of sclerotized tooth-like projections along the margin; marginal cell much more than its own length from the wing-tip (Figs. 239 and 240).

   E. **Ammosphex** Wilcke

Last segment of front tarsus less strongly lobed, and widest about two-thirds the distance from the base, the inner claw of this segment with the inner ray longer (Fig. 230); aedoeagus simple, the margin not armed as above 6

6. Labrum slightly if at all visible beyond the apical margin of the clypeus; propodeum hairy; subgenital plate broader than below, of various shapes; digiti of genitalia broadly excised along the inner margin.

F. **Arachnospila** Kincaid

Labrum exserted beyond the clypeus to about half the shorter diameter of the latter, the apical margin of the clypeus evenly, arcuately concave; propodeum not or scarcely hairy; subgenital plate (at least in our species) narrow and strongly keeled apically, basally (internally) with lateral expansions (Figs. 222 and 223); digiti strap-shaped, not excised.

G. **Anoplochares** Banks

A. Subgenus **POMPILUS** Fabricius

Pompilus Fabricius, 1798, Suppl. Ent. Syst., pp. 212, 246-252. [Type: *Pompilus pulcher* Fabricius, 1798; fixed by Opinion 166 of the Internat. Comm. Zool. Nomen., 1945.]—Wilcke, 1943, Overdr. Med. Landbouwhoogeschool Wageningen, 47: 46.

Psammochares Sustera, 1913, Verh. zool.-bot. Ges. Wien, 62: 210. [*Nec* Latreille, 1796.] [Type: *Sphex plumbea* Fabricius, 1787.]

The subgenus *Pompilus* is here equivalent to the genus *Pompilus* as interpreted by Wilcke (1943) in his monograph of the Pompilidae of the Netherlands. As thus restricted, it includes the widely distributed Old World species *plumbeus* Fabricius and its varieties, and several closely allied species. None of the North American species can be considered consubgeneric with *plumbeus*.

Subgeneric characters.—Mandibles unidentate in both sexes. Clypeus large, wider than the lower front, almost completely covering the labrum. Eyes converging above somewhat in the female; front with an impressed line from the front ocellus to the antennal bases. Malar space present, short. Temples well developed, bearing numerous white hairs.

Pronotum rather short, the sides, seen from above, subparallel; posterior margin subangulate. Postnotum a very narrow band. Propodeum without a well-defined posterior declivity, and without erect hairs. Front tarsus of female with a comb of strong, flat spines; basitarsus rather short, not longer than the two following segments together, bearing three comb-spines, and in addition two long, slightly more slender spines on the inner side, one about midway and one at the apex. Apical segment of front tarsus of male unmodified, nearly parallel-sided (Fig. 226). All the claws of both sexes dentate, those of the male rather weakly so. Apical tarsal segments of female with a complete row of minute spines on the median line beneath, the

spines much smaller than those beneath the other tarsal segments and visible only under high magnification. Pulvillar comb of both sexes consisting of about 8 to 12 unusually stout setulae. Fore wing with three submarginal cells.

Male subgenital plate (Fig. 201) with a pair of short appendages on the sides near the base, visible only upon dissection. Male genitalia (Fig. 171) with the basal hooklets entirely wanting; aedeagus simple, without setae or chitinized teeth; digiti short, subspatulate, the apex with a fringe of setae; parameres long and rather broad, the squamae not prominent.

Biology.—*Pompilus plumbeus* is a common psammophilous species of Europe, and preys upon a variety of spiders, most commonly Lycosidae. A summary of the known facts concerning its biology is given by Richards and Hamm.[3]

Distribution.—Palaearctic, Ethiopian, Oriental, and Australian Regions. There are no Nearctic species.

B. Subgenus **HESPEROPOMPILUS** Evans

Hesperopompilus Evans, 1948, Proc. Ent. Soc. Wash., 50: 141-149. [Type: *Pompilus orophilus* Evans, 1947; original designation.]. [Subgenus of *Pompilus*.]—Dreisbach, 1949, Ent. Amer., 29: 4, 6, 10, 42, fig. 23 (not fig. 22 as stated). [Genus.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 933.

This is a small group, containing five known species, all western and all apparently rare. It is probably a relict group somewhat related to *Agenioideus* and *Evagetes*. The pulvillar comb is not strongly developed, though sometimes slightly more so than in those genera; the delicate build of the body and slender appendages suggest *Agenioideus*; the usually bluish vestiture and the short antennae of the male suggest *Evagetes*. The closest affinities of the group are, however, probably with *Pompilus s. str.*; the male subgenital plate has a pair of basal palpus-like structures as in that group,[4] and there are many other structural similarities.

Subgeneric characters.—Small wasps, 5 to 10 mm. in length. Color black or black and red; pubescence often extensively silvery, in some species almost entirely deep blue-violet. Front and vertex scarcely to rather densely hairy;

[3] Richards, O. W., and A. H. Hamm, 1939, Trans. Soc. Brit. Ent., 6: 74.

[4] In the original description of *Hesperopompilus*, I stated that I knew of no other Pompilini possessing these structures on the subgenital plate. However, I have since discovered their presence in *Pompilus s. str.*, and also in the genus *Aporinellus*, probably a derivative of *Pompilus s. str.*

propodeum with or without erect hairs. Mandibles of female weakly bidentate, of male unidentate. Clypeus of male convexly rounded apically, that of the female either rounded or truncate. Malar space very short; temples not strongly developed; front and vertex of moderate breadth to fairly broad. Antennae of female elongate, the third segment at least four times as long as thick, and equal to at least .75 times the upper interocular distance. Antennae of male relatively less elongate, segment three from 1.4 to 2.5 times as long as thick.

Pronotum variable, its posterior margin never sharply angulate. Propodeum of the female with a fairly well defined, slightly concave posterior declivity. Front basitarsus of female longer than the two following segments together, bearing three (rarely four) long and very slender comb-spines, and no additional long spines. Apical tarsal segments without spines beneath in both sexes. Last segment of front tarsus of male (Fig. 227) only very vaguely if at all produced on the inner margin, almost parallel-sided; inner claw of this segment bifid, the rays widely separated; outer claw of this segment and of all the remaining tarsi dentate. Pulvillar comb of at most 15 rather weak setulae. Fore wing with the second and third submarginal cells both four-sided, both somewhat narrowed above.

Abdomen of female stout, subfusiform, in resting position not exceeding in length the head and thorax together. Abdomen of the male much more slender. Male subgenital plate with two small, palpus-like structures, apparently consisting of matted setae, one on each side near the base, visible only upon dissection. Genitalia with the basal hooklets either single or absent, if present not especially hook-shaped, the apex merely rectangular; digiti shaped much as in *Pompilus s. str.*; parapenials very stout, compressed, in lateral view rather wide; aedoeagus variously developed, in one species with a few setae at the apex.

Distribution.—Western North America, from Lower California and New Mexico to Alberta. Only two of our five species are known from both sexes, and even with these there is no definite evidence that the sexes are correctly associated. The whole subgenus is known at present from only 17 specimens.

Key to Species

Females

1. Apical margin of clypeus arcuately, convexly rounded; pronotum rather long, sloping very gradually in profile; color black, the abdomen and hind femora and tibiae rufous; pubescence in large part silvery.
   1. **rufopictus** Evans

   Apical margin of clypeus truncate; pronotum short and sloping steeply in front; color black, rendered rather conspicuously bluish or blue-green by the pubescence 2

2. Front rather broad, the middle interocular distance varying from .58 to .60 times the transfacial distance; size larger, about 10 mm.; postocellar line equal to or less than the ocello-ocular; third antennal segment equal to from .80 to .9 times the upper interocular distance.
2. **jacintoensis** Evans

Front narrower, the middle interocular distance varying from .50 to .54 times the transfacial distance; size smaller, 6.5 to 8.5 mm.; postocellar line greater than ocello-ocular line; third antennal segment subequal in length to the upper interocular distance .....3. **orophilus** Evans

Males

1. Posterior pronotal margin with a narrow pale stripe; third antennal segment about twice as long as thick, or slightly longer; aedoeagus not parallel-sided, the margins somewhat sinuate 2

Posterior pronotal margin without a pale stripe, though sometimes with a line of pale pubescence; third antennal segment only about 1.5 times as long as its greatest thickness; aedoeagus slender, the margins parallel 3

2. Subgenital plate moderately broad, tapering apically (Fig. 202); parameres of genitalia short, with a tuft of long hairs at the apex; parapenials strongly curved; aedoeagus with an abrupt apical expansion which bears a transverse ridge (Fig. 173); size larger, about 6.5 mm.
2. **jacintoensis** Evans

Subgenital plate very slender, nearly linear (Fig 203); parameres longer, the apex with only short hairs; parapenials only slightly curved; aedoeagus only slightly expanded apically, without such a ridge (Fig. 174); size smaller, about 5 mm. .....3. **orophilus** Evans

3. Propodeum not hairy, the front but slightly so; subgenital plate narrow basally, broadened beyond the base, the apex tapering (Fig. 204); parameres shorter than the aedoeagus, not expanded basally (Fig. 176); size smaller, about 5 mm. .....4. **boharti** new species

Propodeum somewhat hairy, the front densely hairy; subgenital plate broad, the apex broadly rounded (Fig. 205); parameres longer than the aedoeagus, basally somewhat expanded (Fig. 175); size larger, about 9 mm. .....5. **evagetoides** new species

1. Pompilus (Hesperopompilus) rufopictus Evans

Pompilus (*Hesperopompilus*) *rufopictus* Evans, 1948, Proc. Ent. Soc. Wash., 50: 144-146. [Type: ♀; Dos Palmas, Riverside Co., Calif., 8 May 1932 (R. M. and G. E. Bohart); C.A.S. no. 5951.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

This tiny and attractive *Pompilus* is still known from only one specimen. It may be recognized at once by its color and by the

shape of the clypeus, the apical margin of which is convexly rounded.

FEMALE.—Length 6.5 mm. Color black; apical two-thirds of the mandibles and lower portion of the clypeus dull ferruginous; front and middle legs brownish; femora and tibiae of hind legs, except the joints, bright rufo-ferruginous; abdomen bright rufo-ferruginous except the extreme base of the first segment and apex of the last, which are somewhat infuscated. Entire body clothed with a fine, pale pubescence, which is more coarse and conspicuously silvery on the clypeus, front, anterior slope and posterior margin of the pronotum, sides of the scutellum, metanotum, posterior slope of the propodeum, and posterior half of the hind coxae. Wings nearly hyaline, the outer margin of the fore wing broadly banded with brownish. Clypeus front, and vertex with a few dark hairs; temples and propleura with some short, pale hair; body otherwise without erect hairs except for a few dark setae on the apical abdominal segment.

Clypeus 2.5 times as broad as high, its apical margin evenly, convexly rounded. Front rather narrow, the middle interocular distance .56 times the transfacial distance; inner orbits converging very slightly above. Postocellar line slightly greater than the ocello-ocular line. Antennae very long and slender, the first four segments in a ratio of about 2:1:4:3, segment three about equal in length to the upper interocular distance.

Pronotum rather long, its anterior slope very low and even, its posterior margin subarcuate. Slope of the propodeum low, slightly steepened behind, the declivity slightly concave; median line distinctly impressed. Front tarsus slender, with a comb of long and very slender spines, the apical basitarsal spine about as long as the second tarsal segment. Pulvillar comb of about seven weak, diverging setulae. Fore wing with the transverse median vein meeting the media slightly beyond the origin of the basal; stigma short; marginal cell rather long, about 1.2 times its own length from the wing-tip; second submarginal cell nearly twice as broad as high, narrowed by one-third above; third submarginal cell about as broad as high, narrowed by two-thirds above.

MALE.—Unknown.

Distribution.—Known only from the type locality.

Specimens seen: 1 ♀. CALIFORNIA: Riverside Co., Dos Palmas, 8 May 1932 (R. M. & G. E. Bohart) [type, CAS].

2. **Pompilus (Hesperopompilus) jacintoensis** Evans

Pompilus (*Hesperopompilus*) *jacintoensis* Evans, 1948, Proc. Ent. Soc. Wash., 50: 146-148. [Type: ♀; San Jacinto Mts., Calif., July 1912 (J. C. Bridwell); U.S.N.M. no. 58,631.]—Evans, 1951, U. S. Dept. Agr., Monogr. 2, p. 934.

This species closely resembles *orophilus*, but a number of morphological characters, as indicated in the key, readily distinguish it. The pulvillar comb is somewhat more strongly developed than in the other species of the subgenus.

FEMALE.—Length 10 (8.5-12) mm. Color black, the entire body rendered by the pubescence a deep Prussian blue, fading to blue-violet in older specimens. Wings rather heavily infuscated, slightly darker along the outer margin, somewhat violaceous. Clypeus, front, vertex, temples, and propleura with considerable short, dark hair; pronotum and front coxae somewhat hairy, the remaining coxae and the remainder of the thoracic dorsum slightly so; propodeum with numerous erect hairs; abdomen slightly setose apically.

Clypeus 2.4 to 2.7 times as broad as high, its apical margin truncate. Front rather broad, the middle interocular distance varying from .58 to .6 times the transfacial distance. Eyes converging slightly above, the upper interocular distance about .9 the lower. Postocellar line equal to or slightly less than the ocello-ocular line, the ocelli forming an angle in front which may be slightly greater or less than a right angle. Antennae long and slender, the first four segments in a ratio of about 3 : 1 : 5 : 4, segment 3 equal to from .8 to .9 the upper interocular distance.

Pronotum short, sloping strongly in front, its posterior margin arcuate or very feebly angulate. Postnotum reduced to a thin transverse line. Propodeum rather convex, short, the declivity well defined and slightly concave; median line lightly impressed in front. Front tarsus with a comb consisting of three long, slender spines, the apical basitarsal spine about as long as the second tarsal segment, or slightly longer. Pulvillar comb of about 15 fairly strong, subparallel setulae. Fore wing with the transverse median and basal veins interstitial or nearly so; marginal cell of moderate length, from 1.3 to 1.5 times its own length from the wing-tip, the radial vein angled at the third transverse cubital vein. Second submarginal cell much wider than high, narrowed by half or slightly less above; third submarginal cell narrowed by from .7 to .9 above.

MALE.—Length 6.5 mm. Color black, the posterior margin of the pronotum with a pale yellowish stripe, narrowly interrupted medially. Pubescence deep bluish or blue-violet as in the female, except on the lower front, lower side of the scape, posterior slope of the propodeum, and the posterior coxae behind, where it is silvery. Wings subhyaline, outer margins of the front wings broadly infuscated. Clypeus, front, vertex, temples, and propleura with numerous short pale hairs; remainder of body practically devoid of erect hairs.

Clypeus 1.7 times as broad as high, its apical margin convexly rounded. Front rather narrow, the middle interocular distance about .55 times the transfacial distance; eyes diverging slightly above. Postocellar line slightly

less than the ocello-ocular. Antennae of moderate length, the first four segments in a ratio of about 2:1:2:2, segment 3 about 2.3 times as long as thick. Posterior pronotal margin subangulate. Median line of propodeum vaguely impressed. Last segment of front tarsus shown in Fig. 227. Venation about as in the female; second submarginal cell only slightly narrowed above, the third strongly so.

Abdominal sternites 4 and 5 slightly arcuately emarginate posteriorly; sternite 6 with a broad V-shaped emargination. Subgenital plate (Fig. 202) shaped somewhat like an arrowhead; basal sclerite rather broad, partially overlying the palpus-like processes. Genitalia (Fig. 173) characterized by the very short parameres bearing several long setae at the apex; parapenials strongly curved, somewhat S-shaped; aedoeagus constricted just before the apex, which is narrowly and abruptly expanded, this expansion appearing to bear a transverse ridge.

Distribution.—Lower Sonoran fauna, southern California and Lower California.

Specimens seen: 8 (7 ♀♀, 1 ♂). CALIFORNIA: Los Angeles Co., 1 ♂, Pomona Mts., Sept. (H. C. Fall) [MCZ]; 1 ♀, Camp Baldy, 11 July 1950 [CIS]; Riverside Co., 1 ♀, San Jacinto Mts., July 1912 (J. C. Bridwell) [USNM]; San Diego Co., 4 ♀♀, 25 June-10 July [Coll. H. A. Hill, HEE]. MEXICO: Baja California, 1 ♀, Cedros Island, 3 June 1925 (H. H. Keifer) [CAS].

3. Pompilus (Hesperopompilus) orophilus Evans

Pompilus orophilus Evans, 1947, Ent. News, 58: 14-16. [Type: ♀; Raton, N. Mex., 7000 feet, 12 Aug. 1946 (H. E. Evans); M.C.Z.]

Pompilus (Hesperopompilus) orophilus Evans, 1948, Proc. Ent. Soc. Wash., 50: 148-149.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

Hesperopompilus orophilus Dreisbach, 1949, Ent. Amer., 29: 42, pl. V, fig. 23 (not Fig. 22 as stated).

This species is colored like the preceding, but is somewhat smaller. The front of the female is more narrow in proportion to the eyes; the pulvillar comb is weakly developed; the marginal cell is nearly twice its own length from the wing-tip; the subgenital plate of the male is extremely narrow.

FEMALE.—Length 7.5 (6.5-8.5) mm. Color black, the body rendered a deep Prussian blue or a rich blue-green by the pubescence. Wings moderately infuscated, slightly darker along the outer margin, somewhat violaceous. Clypeus, front, vertex, temples, and propleura with fairly abundant dark hairs; pronotum, front coxae, and tip of abdomen slightly hairy.

Clypeus about 2.3 times as broad as high, its apical margin truncate. Front rather narrow, the middle interocular distance varying from .50 to .54

times the transfacial distance. Inner orbits subparallel, the upper and lower interocular distances nearly equal. Postocellar line greater than the ocello-ocular as 6 : 5. Antennae long and slender, the first four segments in a ratio of about 6 : 2 : 9 : 7, the third segment subequal in length to the upper interocular distance.

Pronotum short, sloping rather steeply in front, the posterior margin arcuate. Postnotum fairly long, nearly as long as the metanotum, showing faint transverse striations, with a median impression on each side of which it is very slightly arcuately broadened. Propodeum sloping rather evenly, the declivity not clearly defined; median line distinctly impressed. Front basitarsus with 3 or 4 slender comb-spines, the apical one about as long as the second tarsal segment. Pulvillar comb of about 9 weak, diverging setulae. Fore wing with the transverse median vein meeting the media slightly before the basal; stigma very short; marginal cell short, nearly or fully twice its own length from the apex of the wing. Second submarginal cell considerably broader than high, narrowed by half or slightly more above; third submarginal cell shorter both above and below than the second, narrowed by half or slightly more above.

Male.—Length 5 mm. Posterior margin of the pronotum with a narrow band of pale yellowish, interrupted medially; body otherwise black, rendered by the pubescence a rather brilliant blue-violet, except on the following parts, where it is silvery: clypeus, antennal scape below, front, temples, coxae, pronotum in greater part, a posterior band on the mesonotum, sides of the scutellum, metanotum, mesopleura, upper part of the metapleura, posterior slope of the propodeum (where it is very coarse), and broad basal bands on the first three abdominal segments. Wings hyaline, the fore wings with a fuscous band along the outer margin. Clypeus, front, vertex, temples, propleura, and collar with numerous short, pale hairs; remainder of body without erect hairs.

Clypeus 1.8 times as broad as high, its apical margin arcuately rounded, entirely covering the labrum. Front of moderate breadth, the middle interocular distance .6 the transfacial. Inner orbits diverging above, the upper interocular distance 1.2 times the lower. Ocelli widely separated, forming an acute angle in front; postocellar line greater than the ocello-ocular as 5 : 4. First four antennal segments in a ratio of about 10 : 5 : 9 : 10, segment 3 about twice as long as thick. Pronotum subangulate behind, much shorter than the mesonotum. Postnotum about one third the length of the metanotum. Median line of propodeum impressed. Wing venation about as in the female; radial vein nearly evenly arcuate; transverse median vein meeting the media slightly beyond the origin of the basal.

Abdominal sternite 6 broadly, rectangularly emarginate. Subgenital plate (Fig. 203) very slender apically, nearly linear, its margins fringed with setae; basal sclerite large, though less broad than in *jacintoensis*. Genitalia (Fig. 174) with the parameres long, exceeding the digiti, with only short hairs apically and along the shaft; parapenials simple, stout; aedoeagus with sinuate margins, but not abrubtly expanded and ridged apically as in *jacintoensis*.

Biology.—The type of this species was taken by the author on the gravel bottom of a dried stream bed bordering a meadow at an altitude of about 7000 feet in Raton Pass, New Mexico.

Distribution.—This species appears to inhabit the Transition Zone of western North America, occurring from New Mexico and southern California to Alberta.

Specimens seen: 5 (4 ♀♀, 1 ♂). CALIFORNIA: Los Angeles Co., 1 ♀ (Coquillett) [USNM]; ARIZONA: Pima Co., 1 ♀, Baboquivari Mts., 19 July (H. O. Wright) [UK]; NEW MEXICO: Colfax Co., 1 ♀, Raton, 7000 feet, 12 Aug. (H. E. Evans) [MCZ]; COLORADO: Fremont Co., 1 ♀, Texas Creek, 18 Sept. (R. C. Shannon) [CU]; ALBERTA: 1 ♂, Medicine Hat, 5 July (J. L. Carr) [CNC].

4. **Pompilus (Hesperopompilus) boharti** new species

This species is described from a single male which closely resembles the preceding two species, but which differs in lacking the pale stripe on the posterior pronotal margin, and in the shorter third antennal segment. The terminalia closely resemble those of *jacintoensis,* but the parapenials and aedoeagus are of very different form.

FEMALE.—Unknown; may possibly be *rufopictus,* though structurally this seems unlikely.

MALE (Holotype).—Length 5 mm.; fore wing 3.7 mm. Color wholly black; wings clear hyaline, the veins brown, the fore wing with a narrow pale fuscous marginal band. Pubescence conspicuously silvery on the clypeus, lower half of the front, pronotum, meso- and metapleura, coxae, posterior corners of the mesonotum, sides of the scutellum, metanotum, propodeum, and bases of the first two abdominal segments; pubescence elsewhere brownish. Vertex, temples, and propleura each with a few short hairs, the body otherwise practically devoid of erect hair.

Clypeus convex, 1.7 times as broad as high, its apical margin rounded. Front very broad; middle interocular distance .63 times the transfacial distance. Eyes strongly diverging above; middle interocular distance 1.3 times the lower interocular distance; upper interocular distance 1.25 times the lower. Ocelli small and widely separated; postocellar line : ocello-ocular line about as 5 : 4. Vertex raised rather strongly in an even arc above the tops of the eyes; temples very narrow. Antennae rather short; first four segments in a ratio of 11 : 4 : 7 : 9, the third segment 1.5 times as long as thick.

Posterior pronotal margin arcuate. Postnotum a narrow transverse band, about a third the length of the metanotum. Propodeum rather convex, with a deeply impressed median line. Legs weakly spinose; pulvillar comb very

weakly developed. Anal vein of hind wing meeting the media well before the origin of the cubitus. Fore wing with the transverse median vein meeting the media slightly beyond the origin of the basal. Stigma short; marginal cell long and somewhat pointed apically, removed from the wing-tip by slightly less than its own length. Second submarginal cell 1.8 times as broad as high, narrowed slightly above; third submarginal cell 1.3 times as broad as high, narrowed by about half above.

Abdomen cylindrical, very slender. Emargination of sternite 6 broad and deep. Subgenital plate (Fig. 204) with the basal sclerite rather broad; basal processes slender, well developed; main portion of plate shaped somewhat like an arrowhead. Genitalia (Fig. 176) with the parameres short, subapically with a small, chitinized elevation, the apex setose; digiti slightly exceeding the parameres, with several prominent setae on the upper, outer margin; basal hooklets absent. Parapenials slender, more or less compressed, and the apical half somewhat produced ventrally; aedoeagus simple, slender, parallel-sided.

Holotype.—CALIFORNIA: San Diego Co., ♂, Borego, 5 April 1940 (R. M. Bohart) [CAS].

5. **Pompilus (Hesperopompilus) evagetoides** new species

This is a somewhat larger species of *Hesperopompilus* than any of the others; the pubescence is conspicuously bluish, ornamented with silvery. It bears considerable superficial resemblance to certain species of *Evagetes,* hence the specific name. The subgenital plate is unusually broad, and the genitalia very distinctive. The species is known from two specimens from one locality in Lower California.

FEMALE.—Unknown.

MALE (Holotype).—Length 8 mm.; fore wing 7 mm. Color wholly black; wings subhyaline, the outer margins with a fuscous band. Pubescence dark, conspicuously reflecting deep blue-violet, except silvery on the following parts: clypeus, lower front, temples, anterior slope and posterior margin of the pronotum, sides of the scutellum, metanotum, posterior slope of the propodeum, hind coxae in part, upper sides of the middle and hind tibiae, and median semicircular spots on the apices of the first four abdominal tergites. Clypeus, front, vertex, and temples with rather dense, short, brownish hairs; front coxae and pronotum slightly hairy; propodeum with a considerable amount of dark erect hair; venter with scattered inconspicuous setae.

Clypeus convex, 1.8 times as broad as high, its apical margin rounded. Front convex, broad, the middle interocular distance .63 times the transfacial. Eyes diverging slightly above, the upper interocular distance 1.15 times the lower. Ocelli forming an obtuse angle in front, the postocellar

and ocello-ocular lines about equal. Vertex raised slightly above the tops of the eyes; head flattened immediately behind the eyes. Antennae of moderate length, the first four segments in a ratio of 15:6:10:14, the third segment 1.4 times as long as thick; outer flagellar segments about twice as long as thick.

Posterior pronotal margin arcuate. Postnotum a mere line, almost absent. Slope of the propodeum low and even, the median line not impressed. Hind wing with the anal and cubital veins interstitial on the media. Fore wing with the transverse median vein meeting the media slightly before the origin of the basal. Stigma short; marginal cell removed from the wing-tip by approximately its own length. Second submarginal cell 1.7 times as broad as high, narrowed by about half above; third submarginal cell not quite as wide as the second, 1.5 times as wide as high, narrowed by three-fourths above.

Abodmen slender, subfusiform; sternites 4 and 5 arcuately emarginate apically. Subgenital plate (Fig. 205) broad, nearly parallel-sided, the apex broadly rounded; basal palpus-like appendages well developed. Genitalia (Fig. 175) with the parameres the longest of the appendages, with a broad expansion near the base which is clothed on the dorsal surface with setae which are angled at their apices; apical half of the parameres slender, the outer margin setose. Volsellar digitus short, subspatulate apically, the disc and upper, outer margin with numerous erect hairs; basal hooklets not hook-like, but rectangular at their apices. Parapenials stout, strongly compressed, apically strongly curved ventrally. Aedoeagus slightly surpassing the parapenials, slender and parallel-sided, the apex with several prominent setae.

The single paratype is 10 mm. in length and has a pale stripe along the upper side of the hind tibia for most of its length. The middle interocular distance is .60 times the transfacial distance; the third submarginal cell is triangular. In other respects it closely resembles the type. This specimen is lacking both antennae beyond the fifth segment. Both type and paratype are lacking the sixth abdominal segment, the apical tergite, and the basal plate of the subgenital plate, the latter not being shown in Fig. 205 for this reason.

Holotype.—MEXICO: Baja California, ♂, 20 miles north of Mesquital, 27 Sept. 1941 (E. S. Ross & R. M. Bohart) [CAS].

Paratype.—1 ♂, same data as type [ANSP].

C. Subgenus **XEROCHARES** new subgenus

GENOTYPE: *Pompilus expulsus* Schulz, 1906.

This new subgenus is proposed to accommodate a single species which cannot be placed in any of the existing subgenera. In

some respects, such as the short malar space, the long white hairs on the temples, and the stout, flat spines of the tarsal comb, it resembles *Pompilus s. str.* In other respects it differs considerably from this subgenus. The apical tarsal segment of the female has from 1 to 3 strong spines beneath, but these are near the base, leaving the apical half bare. The last segment of the front tarsus of the male is parallel sided, but both claws are bifid. The subgenital plate lacks the basal appendages of *Pompilus* and *Hesperopompilus*; the basal hooklets of the genitalia are well developed and single.

Subgeneric characters.—Medium-sized wasps, 9 to 17 mm. in length, of heavier build than the preceding two subgenera. Temples, propleura, front coxae, mesopleura, and propodeum with abundant white hair. The single known species is black with the abdomen wholly rufo-ferruginous, and is extensively mottled with a heavy glaucous-gray pubescence. Head thin, especially in the male, the temples not well developed; head of male triangular in outline. Mandibles of female bidentate, of male unidentate. Clypeus truncate below, almost entirely concealing the labrum. Mandibles at base not reaching the eyes, leaving a short malar space.

Pronotum short, its posterior margin arcuate; postnotum a narrow band. Front basitarsus of female with 3 long, flattened spines, the one at the apex longer than the second tarsal segment, without other long spines on this segment. Apical tarsal segment of the female with from one to three strong spines beneath near the base of the segment. Last segment of front tarsus of male parallel-sided, both claws bifid (Fig. 228). Pulvillar comb well developed, in the female of over 20 setulae, in the male of about 12, the setulae slender but rather long. Anal and cubital veins of the hind wing nearly interstitial on the media. Transverse median vein of the fore wing meeting the media slightly basad of the basal. Stigma very short; marginal cell about its own length from the wing-tip.

Male subgenital plate (Fig. 206) without basal appendages. Genitalia (Fig. 172) of simple structure; basal hooklets strong, single; parameres very slender; digiti devoid of setae on the apical fourth; aedoeagus slender and elongate, without setae or spines.

Distribution.—Lower Sonoran fauna of southern Arizona and western Mexico.

1. Pompilus (Xerochares) expulsus Schulz

Pompilus connexus Fox, 1893, Proc. Calif. Acad. Sci., (2)4: 23. [Lectotype: ♀; San José del Cabo, Baja California, Mexico (Gustav Eisen); C.A.S. no. 238.][5] [*Nec* Cresson, 1869.]

[5] I have not seen the type of this species, but have seen a female paratype [ANSP].

Pompilus expulsus Schulz, 1906, Spolia Hymen., p. 170. [New name for *connexus* Fox, *nec* Cresson.]

Psammochares arizonica Banks, 1910, Jour. N. Y. Ent. Soc., 18: 115 [Type: ♀; Palmerlee, Arizona, May; M.C.Z. no. 13,692.]

Psammochares (Psammochares) arizoniensis [*sic!*] Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.

Pompilus rubriventris Bradley, 1944, Notulae Naturae, Acad. Nat. Sci. Phila., no. 145, p. 9. [New name for *connexus* Fox, *nec* Cresson.]

Pompilus (Pompilus) expulsus Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 933.

The wholly bright rufous abdomen and heavy grayish pubescence of this species, combined with the features which set it apart in a subgenus of its own, strikingly separate this form from all other native species of *Pompilus*. It bears considerable superficial resemblance to *Anoplius (Arachnophroctonus) apiculatus apiculatus* (Smith), and overlaps the range of that species.

Female.—Length 15 (12.5-17) mm. Color black; abdomen, except the extreme base of the first segment, bright rufo-ferruginous. Wings lightly infuscated, with a distinct darker band along the outer margin. Greater part of the body and even the appendages clothed with a heavy, grayish-glaucous pubescence, replaced on the following parts with a finer, brownish pubescence: antennae beyond the first two segments; a stripe across the vertex; a stripe on the upper side of the femora; stripes on the tibiae above and below, the basitarsi below, and all the remainder of the tarsi; a broad stripe across the pronotum, interrupted medially; tegulae; anterior half of the mesonotum; disc of the scutellum; and a vaguely defined area on the anterior part of the propodeum. Pubescence of the abdomen very fine, silvery. Scape with a few short, pale hairs below, and a few dark hairs above; clypeus, front, and vertex with abundant short hairs, mixed dark and light; temples, propleura, and front coxae with abundant rather long pale hairs; pronotum with a few dark hairs near the hind margin, elsewhere above and on the sides clothed with pale hairs; mesopleura, metanotum, propodeum, and base of the first abdominal tergite with abundant, mostly whitish hairs; abdominal sternites 3 to 6 and tergite 6 each with a few strong, dark setae.

Clypeus about 2.5 times as broad as high, the apical margin very slightly concave. Front of moderate breadth, the middle interocular distance about .58 times the transfacial distance. Inner orbits convergent above, the upper interocular distance about .8 the lower. Ocelli forming an acute angle in front, the postocellar line usually slightly less than the ocello-ocular. Antennae rather long, the first four segments in a ratio of about 6 : 2 : 10 : 7, segment 3 equal to about .9 the upper interocular distance.

Propodeum sloping very gently, more steeply declivous behind, the median line usually rather vaguely impressed. Fore wing with the radial vein somewhat angled at the third transverse cubital vein; second and third submarginal cells both about 1.5 times as broad as high, the second narrowed slightly above by the arcuation of the first transverse cubital vein, the third narrowed more strongly above by the arcuation of the third transverse cubital vein.

MALE.—Length 11.5 (9-13.5) mm. Color black; abdomen, except the extreme base of the first segment, bright rufo-ferruginous; posterior margin of the pronotum with a narrow yellowish stripe. Wings colored as in the female. Pubescence as in the female, except that the pattern on the legs is more irregular. Scape with white hairs below and a few dark ones above; erect hairs on the head and thorax distributed much as in the female; abdomen with pale hairs on the base of the first tergite and a few short dark ones on the apical sternites.

Head very thin, flattened immediately behind the eyes. Malar space nearly as long as the antennal pedicel. Clypeus slightly over twice as broad as high. Middle interocular distance about .6 the transfacial distance; eyes diverging very slightly above. Ocelli rather large, forming a right or acute angle in front; postocellar line less than the ocello-ocular line as 2:3. First four antennal segments in a ratio of about 5:2:5:5. Propodeum rather long, the sides gradually converging behind; median line faintly impressed. Venation as in the female.

Abdominal sternite 6 with a shallow U-shaped emargination. Subgenital plate (Fig. 206) of moderate breadth, somewhat raised along the median line, the apex truncate. Genitalia (Fig. 172) with the appendages subequal in length, all rather slender. Parameres very slender, slightly curved, the outer margin short-setose. Digitus slender, slightly and gradually expanded toward the apex, which is subtruncate, the apical fourth bare, the remainder clothed with short setae. Parapenials simple, straight; aedoeagus narrowly fusiform, the apex deeply cleft.

Distribution.—This is a Lower Sonoran form, known only from southern Arizona and from Baja California. It will doubtless be found to occur in other parts of western Mexico, and perhaps in southern California.

Specimens seen: 12 (4 ♀♀, 8 ♂♂). ARIZONA: Cochise Co., 1 ♂, Reef, 14 Nov. (Biederman) [ANSP]; 1 ♀, Palmerlee, May [MCZ]; Maricopa Co., 2 ♂♂, Phoenix, 15 Oct. (R. H. Crandall) [CU]; Pima Co., 1 ♀, 1 ♂, Baboquivari Mts., 30 June, 18 Aug. (O. C. Poling) [CAS]; 1 ♂, Tucson (F. H. Snow) [UK]; 1 ♂, Sycamore Canyon, Santa Catalina Mts., 3800 feet, 20 Aug. [AMNH]; MEXICO: Baja California, 1 ♀, Angeles Bay, Gulf of California, 27 June (E. P. VanDuzee) [CAS]; 2 ♂♂, La Paz, 3 June (E. P. VanDuzee) [CAS]; 1 ♀ San José del Cabo (G. Eisen) [ANSP].

D. Subgenus **PERISSOPOMPILUS** new subgenus

GENOTYPE: *Pompilus (Ammosphex) phoenix* Evans, 1948.

Although I originally considered *phoenix* an aberrant member of the subgenus *Ammosphex*, it forms an exception to many of the characteristics of that group, and it now seems best to remove it to a new subgenus. This action has been precipitated by the discovery of an interesting new species closely allied to *phoenix*, yet differing still more radically from any of the other subgenera of *Pompilus*. In this new species the third submarginal cell of the fore wing is entirely wanting, the front tarsus is very short, and the body is heavily banded with silvery pubescence. The beginnings of all of these tendencies can be observed in *phoenix*. All in all, this seems to be a rather highly evolved, though probably relict, subgenus of *Pompilus*. In many of its characters it approaches *Hesperopompilus*, though the double basal hooklets of the male genitalia and perhaps the venation appear to ally it with *Ammosphex*.

Subgeneric characters.—Very small wasps, 3 to 11 mm. in length. Color black, except the apical half of the mandibles more or less ferruginous. Body with some fine, light hair on the temples, propleura, and sometimes the pronotum, but otherwise smooth and devoid of erect hairs, even on the apical abdominal segments of the female. Pubescence either wholly dark, or more often in considerable part silvery; abdomen with a tendency to have silvery bands at the apices of the basal tergites, in which the pubescence diverges from the median line (reduced or absent in the ♀ *phoenix*).

Mandibles unidentate in both sexes. Clypeus truncate below in both sexes, in the female somewhat wider than the lower front. Front and vertex rather dull, the surface minutely granulo-punctate; line from the antennal bases to the front ocellus deeply impressed. Ocelli widely separated, the postocellar line consideraly greater than the ocello-ocular. Antennae short or of moderate length; segment 3 in the female at least three times as long as broad, and longer than the fourth; segment 3 in the male not or scarcely twice as long as thick.

Posterior margin of the pronotum varying from arcuate to rather distinctly angulate. Postnotum rather large, usually as long as the metanotum medially. Median line of propodeum deeply impressed. Legs weakly to moderately spinose; ultimate tarsal segments without spines beneath, or with not more than 3 small spines on the basal half. Front basitarsus of female short, not longer than the two following segments together, bearing only two comb-spines. Pulvillar pad of moderate size, the comb greatly reduced, of only a few very short setulae. Fore wing with the marginal cell short, at least 1.5 times its own length from the wing-tip, usually more; radial

vein somewhat angled at the second transverse cubital vein. Second submarginal cell quadrangular, somewhat wider than high, receiving the first recurrent vein not far from the middle; third submarginal cell very much smaller than the second, triangular, often petiolate, in one species wholly absent; second recurrent vein received by the third submarginal cell near the middle when this is present, or near the outer corner of the second submarginal cell when the third is absent. (Wings shown in Figs. 237 and 238.)

Abdomen of the female stout, subfusiform, the tip smooth or with some very short, inconspicuous setae. Abdomen of male short, somewhat arched, the apical segments normally somewhat telescoped into the basal four. Sternite 6 (Fig. 178) with a flat or somewhat depressed elongate median area set off by a carina, apically with a broad and shallow emargination on each side of which it is angularly produced. Subgenital plate (Fig. 207) of moderate breadth, with a pair of tooth-like protuberances near the median line at the extreme base, not visible externally. Genitalia (Fig. 177) with the basal hooklets unusually large and prominent, double; parapenials short and broad; aedoeagus very slender, expanded abruptly at the apex.

Distribution.—This subgenus appears to be restricted to the Lower Sonoran fauna of the southwestern United States and western Mexico.

Key to Species

Fore wing with a small third submarginal cell present; female: apical segment of middle and hind tarsi with two or three small spines beneath, but the legs as a whole weakly spinose; front wings of female wholly somewhat infuscated, violaceous, the body at most weakly banded with silvery pubescence; male: genitalia and subgenital plate as shown in Figs. 177 and 207 ..... 1. **phoenix** Evans

Fore wing with the third submarginal cell absent; female: apical segment of all the tarsi without spines beneath, but the legs as a whole rather strongly spinose; front wings hyaline, the apical fourth contrastingly infuscated; body very conspicuously ornamented with silvery pubescence; male: not as yet known ..... 2. **perfasciatus** new species

1. Pompilus (Perissopompilus) phoenix Evans

Pompilus (Ammosphex) phoenix Evans, 1948, Pan-Pac. Ent., 24: 123-127. [Type: ♂; Phoenix, Arizona, 11 July 1932; C.A.S. no. 5952.]—Dreisbach, 1949, Ent. Amer., 29: 42, pl. v, fig. 22 (not fig. 23 as stated).—Evans, 1950, Trans. Amer. Ent. Soc., 75: 166.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

Despite a considerable amount of variation in size and in facial proportions, this very distinctive species can scarcely be confused with any other. Although only recently recognized, it is not a rare species within its range.

FEMALE.—Length 8.5 (5.5-10.5) mm. Color black; front wings brownish, with a darker marginal band, strongly violaceous; hind wings hyaline, the tip infuscated. Pubescence very fine, somewhat velvety, over most of the body brownish or fusco-violaceous; some specimens are without silvery pubescence, while others have a considerable amount of it, particularly on the front, temples, scutellum, metanotum, propodeum, and occasionally in the form of weak silvery bands at the apices of the basal abdominal tergites, suggesting those of the male.

Clypeus about three times as broad as high, its apical margin truncate, with a narrow raised rim. Front narrow in relation to the eyes, which are large and prominent; middle interocular distance varying from .45 to .57 times the transfacial distance. Inner orbits converging slightly above, the upper interocular distance from .8 to .9 the lower. Ocelli forming about a right angle in front; postocellar line greater than the ocello-ocular line as 4:3. Antennae of moderate length, the first four segments in a ratio of about 3:1:4:3, segment 3 equal to from .65 to 1.0 times the upper interocular distance, usually closer to the latter figure.

Pronotum rather full in the shoulders, usually with a faint median impression, its posterior margin angulate. Propodeum with the slope low in front, posteriorly with a short, oblique declivity; median line strongly impressed. Legs unusually weakly spinose. Tarsal comb with only two spines in a row on the basitarsus; the comb-spines vary in length from 1 to 2 times as long as the width of the tarsus. Apical tarsal segment with from 1 to 3 minute spines beneath near the base, the apical half bare. Cubitus of hind wing arising opposite the tip of the submedian cell or nearly so. Fore wing with the marginal cell only about twice as long as high, at least twice its own length from the wing-tip; third submarginal cell very much smaller than the second, higher than broad, often petiolate. (Wings shown in Fig. 237.)

MALE.—Length 5.5 (3.5-7) mm. Color black; wings clear hyaline, the outer margin of the fore wing with a broad brownish band. Body clothed with a dense, coarse, silvery pubescence on the following parts: lower half of scape, basal half of mandibles, clypeus, front, temples, pronotum, posterior half or more of mesonotum, sides of scutellum, metanotum, propodeum, all the pleurites, coxae, to some extent the trochanters, and femora, first abdominal tergite, and sharply defined broad apical bands on tergites 2, 3, and 4; here and on the propodeum the setulae diverge strongly from the median line. Vertex, front part of mesonotum, disc of scutellum, and remainder of abdomen and appendages with a finer, brownish pubescence.

Clypeus about twice as broad as high, its apical margin truncate. Eyes very large, the front rather narrow between them, the middle interocular distance varying from .5 to .6 the transfacial distance. Eyes diverging noticeably above, the upper interocular distance about 1.2 times the lower interocular. Ocelli prominent, in a large triangle; postocellar: ocello-ocular line about as 3:2. First four antennal segments in a ratio of about 25:10:15:18, segment 3 from 1.3 to 2 times as long as thick. Posterior

pronotal margin broadly angulate or nearly arcuate. Last segment of front tarsus unmodified, parallel-sided, the inner claw strongly curved, bifid, the outer claw dentate. Legs weakly spinose, very thin apically. Venation as in the female; third submarginal cell in all the specimens seen rather long-petiolate.

Abdomen with sternite 6 and the subgenital plate as described under the subgeneric heading and as shown in Figs. 178 and 207. Genitalia (Fig. 177) with the parameres very slender, sparsely setose, not exceeding the other appendages; digiti narrowly subspatulate, clothed with short setae; parapenials rather short and stout, their inner margins excised near the base of the aedoeagus. Aedoeagus with a broad expansion near the base, beyond which it is much more slender, the extreme apex expanded, suggesting the tail of a fish; margins of the aedoeagus somewhat irregular.

Biology.—I have taken males of this species on dried leaves beneath an oak tree which was dripping honeydew. Because of their small size, erratic flight, and somewhat disruptive markings, they are exceedingly difficult to see.

Distribution.—This species is widely distributed in the Lower Sonoran Zone, ranging from western Texas, Utah, and central California south into Mexico.

Specimens seen: 28 (16 ♀♀, 12 ♂♂). Texas: Brewster Co., 9 ♂♂, The Basin, Chisos Mts., 5400 feet, 8-14 July [HEE, CU, ANSP]; Jeff Davis Co., 1 ♀, Fort Davis, 26 July [HEE]; Arizona: Maricopa Co., 2 ♀♀, 1 ♂, Phoenix, July, Oct. [CAS, CU]; Utah: San Juan Co., 1 ♀, Bluff, 7 July [MCZ]; California: Alameda Co., 1 ♀, Tesla, 15 Oct. [CIS]; Calaveras Co., 1 ♀, Mokelumne Hill, Oct. [CAS]; Contra Costa Co., 1 ♀, Antioch, 10 Sept. [CAS]; Fresno Co., 1 ♀, Coalinga, 18 July [USNM]; Imperial Co., 1 ♀, El Centro, 14 June [CIS]; 1 ♀, Palo Verde, 20 Aug. [CAS]; Inyo Co., 1 ♂, Independence, 7 June [USNM]; Kern Co., 1 ♀, Red Rock Canyon, 30 Apr. [CIS]; Kings Co., 1 ♀, Lemoore, 6 Aug. [CU]; Riverside Co., 1 ♀, Indio, 1 Apr. [CIS]; San Bernardino Co., 1 ♀, 1 ♂, Yermo, 28 Apr., 23 May [CIS, UAC]; San Diego Co., 1 ♀, National City, 15 May [MCZ]; Mexico: 1 ♀ (no further data) [USNM].

2. **Pompilus (Perissopompilus) perfasciatus** new species

This remarkable and highly attractive species is described from a single specimen of the female sex. Although obviously related to *phoenix*, it possesses a number of unusual characteristics: the third submarginal cell is wholly wanting; the antennae are unusually short, the third segment equal to only .46 times the upper interocular distance; the body is highly ornamented with silvery pubescence, much as in the male *phoenix*, but much more so than in the female of that species.

FEMALE (Holotype).—Length 5.3 mm.; fore wing 4.5 mm. Color black; front wings clear hyaline on the basal three-fourths, the apical fourth with a broad, contrasting brownish band; hind wings hyaline, the tip slightly clouded. Body clothed almost entirely by a brilliant silvery pubescence, absent only from the vertex, mesonotum, disc of the scutellum, metapleura, apex of the abdomen, outer portion of the legs, and antennal flagellum. This pubescence is particularly strong on the sides of the lower front and clypeus, the temples, the sides of the pro- and mesothorax, hind coxae, and the propodeum; the basal four abdominal segments are completely clothed with sericeous pubescence which is directed backward, except for apical bands on the first three tergites (and to a lesser extent the fourth), where the pubescence is more coarse and diverges strongly from the median line. The body is completely devoid of erect hairs except for a few on the occiput and propleura.

Head much broader than high, the transfacial distance 1.25 times the facial distance, and very thick, the eyes wide and the temples rather strong. Clypeus nearly four times as broad as high, its apical margin broadly truncate. Front of moderate breadth, the middle interocular distance .56 times the transfacial distance. Inner margins of eyes subparallel, the middle interocular distance subequal to the lower, the upper .9 the lower. Vertex broad, rather flat between the tops of the eyes; postocellar line greater than the ocello-ocular line as 5:3. Antennae unusually short for the genus, the first four segments in a ratio of 12:5:12:10, segment three about 3 times as long as its greatest thickness, equal to .46 times the upper interocular distance; outer flagellar segments, except the last, only about 1.5 times as long as thick.

Pronotum short, its posterior margin feebly angulate. Median line of propodeum impressed. Legs rather strongly spinose, but the ultimate tarsal segments without spines beneath. Front basitarsus short, only about 2.5 times as long as its greatest thickness, bearing two comb-spines, each about half the length of the basitarsus and about equal to the length of the second tarsal segment. Hind wing with the cubitus arising well beyond the apex of the submedian cell. Fore wing with the basal vein arising slightly basad of the transverse median vein on the media. Stigma of moderate size; marginal cell short, slightly over twice its own length from the tip of the wing. Second submarginal cell 1.25 times as broad as high, narrowed by a little more than half above by the slight arcuation of the first and second transverse cubital veins, receiving the first recurrent vein .4 of the way from the base, the second recurrent vein .9 the distance from the base; third submarginal cell wanting. (Wings shown in Fig. 238.)

Abdomen short and stout, a little flattened dorsally, heavily banded with silvery pubescence as described above; apical segment slightly depressed, with only some very fine, short, inconspicuous hair.

MALE.—Unknown.

Holotype.—CALIFORNIA: Riverside Co., ♀, Whitewater, 9 July 1950 (J. W. MacSwain) [CAS].

E. Subgenus **AMMOSPHEX** Wilcke

Psammochares (*Psammochares*) *gibbus* group Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, pp. 154, 162, 200.

Ammosphex Wilcke, 1942, Ent. Berichten, 11: 25. [Type: *Pompilus unguicularis* Thomson, 1870; original designation.]—Wilcke, 1943, Overdr. uit Med. Landbouwhoogeschool Wageningen, 47: 12, 47-61. [In part; Netherlands species.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

Anopompilinus Dreisbach, 1949, Ent. Amer., 29: 7, 10, 11, 34, pl. I, fig. 3. [Type: *Anopompilinus michiganensis* Dreisbach, 1949; monobasic.]—Dreisbach, 1950, Amer. Midl. Nat., 42: 723-738.

This and the following two subgenera are rather closely related, and were all included by Wilcke in his genus *Ammosphex*, although there are several earlier names for the group as so defined. These three subgenera probably represent a somewhat recent development of a single line arising somewhere among the more protean subgenera *Pompilus* and *Hesperopompilus*. The two most characteristic features of the subgenus *Ammosphex*, as here defined, are (1) the tendency for the cells of the fore wing to be rather far removed from the outer wing margin, the marginal cell being from 1.3 to 3 times its own length from the wing-tip, and (2) the peculiar structure of the male aedoeagus, which bears along its margin a number of small, tooth-like, pigmented projections.

Dreisbach (1950) has accurately defined the limits of this group in our fauna, and has presented a synopsis of the Nearctic species, with photographs of the male terminalia. He was, however, apparently unacquainted with the European fauna, and with the important papers of Wilcke (1942, 1943). *Pompilus unguicularis* Thomson, the type of *Ammosphex*, is very closely allied to *michiganensis* Dreisbach, and the name *Anopompilinus* Dreisbach must therefore fall as a synonym of *Ammosphex*.

Subgeneric characters.—Small wasps, 3.5 to 12 mm. in length. Color black, the mandibles usually somewhat ferruginous apically, some species with the basal abdominal segments marked with rufous. Body with a variable amount of erect hair, but seldom as much as in the following subgenus; front and propodeum at most moderately hairy. Mandibles unidentate in the male, bidentate in the female. Malar space virtually absent. Labrum exserted only a short distance or not at all beyond the clypeus. Antennae fairly long, segment 3 in the male over twice as long as thick, and as long as segment 4.

Posterior margin of the pronotum distinctly angulate. Postnotum of moderate length, at least half the length of the metanotum. Front tarsus of the female with a comb of short to fairly long spines, the basitarsus always with 3 comb-spines. Apical tarsal segment of the female with a more or less complete row of spines beneath, which are about as long as those beneath the other tarsal segments. Last segment of front tarsus of male strongly asymmetrical, with a lobe on the inner margin which reaches its widest at about the middle of the segment, the outer claw of this segment bifid, the inner bifid and with the inner ray short and rounded (Fig. 229). Pulvillar comb fairly well developed, of about 12 setulae in the female, about 8 in the male. Hind wing with the cubitus arising usually slightly beyond the tip of the submedian cell. Fore wing with the basal vein arising at or slightly before the transverse median vein. Stigma very short; marginal cell short, not more than 2.5 times as long as high, at least 1.3 times its own length from the tip of the wing. Second and third submarginal cells rather small, rarely wider than high, often higher than wide, much narrowed above. (Figs. 239 and 240.)

Subgenital plate of the male variously modified, never with large lateral expansions at the base or with palpus-like processes. Genitalia with the basal hooklets double; parameres long and more or less setose; digiti of rather uniform pattern throughout the group, expanded and curved apically, the disc usually with an area of feeble longitudinal striolations toward the apex. Parapenials rather short, always shorter than the aedoeagus; aedoeagus bearing somewhere along its margins a number of small, pigmented, tooth-like projections, clearly visible under high magnification.

Biology.—Members of this subgenus occur in a variety of habitats, but seem particularly characteristic of wooded places, where they may often be found close to the ground in sunny spots. In such a place it is not uncommon to find several species flying together. They also visit honeydew and flowers to some extent. The prey consists chiefly of Lycosidae. Very little is known of the habits of our native species. Accounts of the habits of the European *unguicularis* and *trivialis* are given by Richards and Hamm.[6]

Distribution.—Holarctic Region; represented in Europe by such species as *Pompilus unguicularis* Thomson, *P. trivialis* Dahlbom, and *P. abnormis* Dahlbom. In our fauna there are eight known species, three of them polytypic.

[6] Richards, O. W., and A. H. Hamm, 1939, Trans. Soc. Brit. Ent., 6: 81-83.

Key to Species

Females

1. Propodeum not hairy or with at most a few very short, inconspicuous hairs on the sides; apical margin of clypeus truncate or slightly arcuately concave (Figs. 233 and 234) 2
Propodeum with at least a few long and rather noticeable erect hairs; clypeus arcuately emarginate apically, though often not deeply so (Figs. 235 and 236) 8
2. Marginal cell very short, removed from the wing-tip by at least twice its own length (Fig. 239); color black or blue-black 3
Marginal cell slightly longer, removed from the wing-tip by less than twice its own length, usually about 1.5 times its own length (Fig. 240); color black or black and red 7
3. Third antennal segment equal to at least .9 the upper interocular distance, usually about equal to it; color blue-black; spines of the tarsal comb distinctly longer than the width of the tarsus 4
Third antennal segment equal to from .6 to .9 the upper interocular distance; color black, the pubescence sometimes reflecting bluish or violaceous; spines of the tarsal comb at most slightly longer than the width of the tarsus 5
4 Integument with a distinct bluish caste, the pubescence usually wholly dark, conspicuously bluish-retulgent or violaceous; Arizona and Utah to California .....4a. **solonus solonus** (Banks)
Integument black or only vaguely bluish, the pubescence with moderately strong bluish or violet reflections, except on the sides of the lower front, where it is silvery; occurring east of the range of the preceding, from eastern Arizona and Texas to Colorado.
4b. **solonus silvivagus** new subspecies
5. Front considerably broader than the two eyes taken together, the middle interocular distance varying from .55 to .61 times the transfacial distance (averaging .58); third antennal segment usually slightly shorter than the first two together; transcontinental in distribution.
1. **angularis** (Banks)
Front only a little wider than the two eyes taken together, the middle interocular distance varying from .53 to .57 times the transfacial distance (averaging .55); third antennal segment subequal to or slightly longer than the first two together; western North America 6
6. Third antennal segment equal to from .6 to .8 the upper interocular distance; pubescence wholly dark, somewhat violaceous; wings strongly violaceous in fresh specimens .....3. **anomalus** (Dreisbach)
Third antennal segment equal to from .75 to .9 times the upper interocular distance; pubescence usually silvery on the sides of the lower front; wings somewhat violaceous or not .....2. **parvulus** (Banks)
7. Base of the abdomen marked with rufous.
5a. **michiganensis michiganensis** (Dreisbach)

Wholly black .....5b. **michiganensis dakota** (Dreisbach)

8. Spines of the tarsal comb not or but slightly longer than the width of the tarsus; apical margin of the clypeus barely emarginate (Fig. 235); antennal segment 3 about equal to the first two together; body less hairy than below 9

Spines of the tarsal comb distinctly longer than the width of the tarsus, or if not so, the clypeus very distinctly emarginate, as in Fig. 236; third antennal segment slightly longer than the first two together; head, thorax, and propodeum rather strongly hairy 10

9. Entirely black .....6a. **imbecillus imbecillus** (Banks)

Base of the abdomen marked with rufous.

6b. **imbecillus ojibwae** new subspecies

10. Longer spur of hind tibia not more than two thirds the length of the hind basitarsus, the setulae on the spurs somewhat more coarse than the usual pubescence of the body (Fig. 224); emargination of the clypeus moderately deep (Fig. 236); integument black.

7. **luctuosus** Cresson

Longer spur of hind tibia more than two thirds the length of the hind basitarsus, the setulae on the spurs small and appressed (Fig. 225); emargination of the clypeus shallow; integument reflecting deep blue, at least in fresh specimens, especially noticeable on the front.

8. **occidentalis** (Dreisbach)

Males

1. Subgenital plate without erect hairs on the median line just before the apex (Figs. 208, 209, and 210); aedoeagus strongly modified, the sinuation of the margins delimiting three arcuately broadened portions along the shaft (*Angularis*-group) 2

Subgenital plate with a pencil, tuft, or series of erect hairs on the median line just before the apex (very short in *solonus*) (Figs. 213-218); aedoeagus simple, the margins not strongly sinuate (*Luctuosus*-group) 4

2. Subgenital plate (Fig. 208) with the sides tapering evenly to a subacute apex; tips of the parameres with long, bushy hairs (Fig. 181).

1. **angularis** (Banks)

Subgenital plate with the sides not tapering evenly to the apex, but somewhat sinuate (not usually evident without dissection); tips of the parameres short-setose 3

3. Subgenital plate (Fig. 210) slender apically, the margins flared out and provided with some rather long hairs toward the base; genitalia (Fig. 180) with the parameres clothed with erect, bristling setae.

3. **anomalus** (Dreisbach)

Subgenital plate (Fig. 209) of somewhat variable form, but in general less slender apically, and without a group of suberect hairs on each side toward the base; genitalia (Fig. 179) with the parameres clothed for the most part with soft, suberect setae .....2. **parvulus** (Banks)

4. Subgenital plate with only some very short setae in a tuft or series near the apex (Figs. 217 and 218); marginal cell about twice its own length from the wing-tip (Fig. 239) 5

Subgenital plate with a pencil, tuft, or series of rather long setae near the apex (occasionally worn or broken off); marginal cell usually less than twice its own length from the wing-tip (Fig. 240) 6

5. Entire disc of the subgenital plate slightly elevated, short-setose (Fig. 217); parameres more slender and sparsely setose apically than below (Fig. 183) .....4a. **solonus solonus** (Banks)

Disc of the subgenital plate not wholly elevated, but only the median line narrowly raised and provided with a series of small setae (Fig. 218); parameres broader and more strongly setose than above (Fig. 184) .....4b. **solonus silvivagus** new subspecies

6. Subgenital plate with two elevated ridges which converge somewhat posteriorly and between which it is flat or slightly concave, subapically with a pencil of setae (Fig. 214) 7

Subgenital plate either flat or with the median line strongly elevated ...8

7. Subgenital plate with a comb of stout setae on each side near the base (not visible externally) (Fig. 211); parameres of genitalia slender; basis volsellaris with a small group of slender setae (Fig. 185).
5a. **michiganensis michiganensis** (Dreisbach)

Subgenital plate with an interrupted series of slender setae on each side near the base (not visible externally) (Fig. 212); parameres rather broad, tapering apically; basis volsellaris with a prominent group of stout setae (Fig 186) .....5b. **michiganensis dakota** (Dreisbach)

8. Subgenital plate more or less keeled, tectiform, near the apex with a tuft or short series of rather long hairs, beyond which the plate slopes rapidly to the apex (Fig. 213) 9

Subgenital plate flat or nearly so 10

9. Wholly black .....6a. **imbecillus imbecillus** (Banks)

Second abdominal tergite marked with rufous.
6b. **imbecillus ojibwae** new subspecies

10. Subgenital plate with a series of prominent setae along the median line (Fig. 215); hind basitarsus compressed; the inner side covered with erect setulae; aedoeagus spined only on the apical one-third (Fig. 188).
7. **luctuosus** Cresson

Subgenital plate with a pencil of setae near the apex (Fig. 216); hind basitarsus unmodified; aedoeagus armed with spines for at least the apical half (Fig. 187) .....8. **occidentalis** (Dreisbach)

Angularis Species-group

In this group the aedoeagus of the male is of unusual form, the sides being strongly sinuate so as to delimit three arcuately expanded lobes along the shaft. The subgenital plate is without the erect hairs so characteristic of the *Luctuosus*-group. The venation is well removed from the outer margin of the wing, the marginal cell usually being at least twice its own length from the wing-tip. The propodeum is without erect hairs, and the clypeus of the female never more than very slightly arcuately concave apically.

The three species comprising this group are very closely allied and not easily separable. The best characters lie in the parameres of the male genitalia, which are distinctly different in the three species. The subgenital plate also shows specific characters, although it is subject to considerable individual variation within each species. The characters used in the key for separating the females of this species-group are of a tentative nature, as I am not certain that they will always properly separate the species.

1 **Pompilus (Ammosphex) angularis** (Banks)

Psammochares angularis Banks, 1910, Jour. N. Y. Ent. Soc., 18: 115. [Type: ♂; Claremont, Calif. (Baker); M.C.Z. no. 13,676.]

Psammochares (Pompiloides) angularis Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.

Pompiloides angularis Banks, 1919, Bull. Mus. Comp. Zool., 63: 235.

Pompilus angularis Strickland, 1947, Canad. Ent., 79: 124. [Drumheller, Alta.]

Anopompilinus angularis Dreisbach, 1950, Amer. Midl. Nat., 42: 734. [Placed in synonymy with *parvulus* Banks.]

Pompilus (Ammosphex) angularis Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

This is our smallest native *Pompilus*. The front of the female averages somewhat broader than in the following two species, and the third antennal segment is usually slightly shorter than the first two combined; the wings are iridescent but rarely wholly violaceous. The male is best identified by the characteristic subgenital plate (Fig. 208) and by the long hairs at the apex of the parameres (Fig. 181). Since this is the only member of the species-group occurring in the eastern United States, eastern specimens can be assigned with little difficulty.

FEMALE.—Length 6.5 (4.5-8) mm. Color black; wings lightly infuscated, broadly darker beyond the cells, reflecting various colors, including green, rose, and violet, but the wings rarely wholly violaceous. Pubescence fusco-violaceous and/or silvery; specimens from the West tend to be mostly dark-pubescent, though usually silvery on the sides of the front, while eastern specimens usually are silvery pubescent over a large part of the head, thorax, and propodeum. Front, pronotum, and front coxae each with a few erect hairs; remainder of thorax, and the propodeum, scarcely or not at all hairy.

Clypeus slightly over three times as broad as high, the apical margin at most very slightly arcuately concave. Front broad, the middle interocular distance varying from .55 to .61 (averaging .58) times the transfacial distance; inner orbits converging slightly above, the upper interocular distance from .8 to .85 times the lower interocular. Antennae of moderate length, the first four segments in a ratio of about 10 : 6 : 19 : 17, the third segment about 3.5 times as long as its greatest thickness, and equal to from .62 to .75 times the upper interocular distance. Postocellar line subequal to or slightly less than the ocello-ocular line.

Propodeum sloping very gradually in front, more steeply behind; median line impressed. Front tarsus with a comb of spines which are not or scarcely longer than the width of the tarsus, the apical spine on the basitarsus about half the length of the second tarsal segment. Marginal cell of the fore wing short, about twice as long as high, from 2.2 to 3 times its own length from the wing-tip. Second and third submarginal cells small, not wider than high, both narrowed by more than half above. Third discoidal cell at least 1.5 times its own length from the outer wing margin.

MALE.—Length 5.5 (4-6.5) mm. Color black; wings hyaline, the outer margin of the fore wing broadly infuscated. Head and thorax in large part finely silvery-sericeous, the abdomen often in part so. Temples, propleura, and front coxae with a few pale erect hairs; front with a few dark hairs; remainder of body not at all hairy.

Clypeus about 2.6 times as broad as high, the lower margin very slightly concave. Front of moderate breadth, the middle interocular distance varying from .57 to .63 times the transfacial distance; inner orbits subparallel or slightly diverging above. First four antennal segments in a ratio of about 24 : 10 : 23 : 24, the third segment about 2.5 times as long as thick. Postnotum expanded dorsally, where it is as long as or slightly longer than the metanotum, depressed on the median line. Propodeum with an impressed median line, sloping more steeply behind. Venation similar to that of the female, but the veins still farther removed from the outer wing margin; marginal cell very short, at least 2.5 times its own length from the wing-tip; third submarginal cell sometimes triangular or petiolate.

Abdominal sternite 6 with a deep V-shaped emargination. Subgenital plate (Fig. 208) simple, rather slender, attenuate apically. Genitalia (Fig. 181) with the parameres considerably exceeding the other appendages, apically acutely pointed and bushy-haired. Digiti subspatulate, the disc

clothed with short setae. Parapenials rather short, nearly straight. Aedoeagus with its margins sinuate, tapering apically to a deeply divided apex; margin armed with scattered short spines on the apical third.

Biology.—This species occurs in sheltered sandy areas and in open woodlands where the soil is light. It has been taken on honeydew and on the flowers of *Clcome.* The species is probably commoner than the records suggest; because of its small size and quick, nervous flight close to the ground, it is scarcely apt to be noticed from the height of a man's head.

Distribution.—This species occurs transcontinentally in the Transition and Upper Austral Zones, with an occasional record from the Canadian and Lower Austral Zones.

Specimens seen: 74 (41 ♀♀, 33 ♂♂). MASSACHUSETTS: Middlesex, Norfolk, and Suffolk Cos., 4 ♀♀, 3 ♂♂, Aug.-Sept. [CAS]; CONNECTICUT: Hartford Co., 4 ♀♀, 4 ♂♂, Aug.-Sept. [HEE, ANSP]; NEW JERSEY: Atlantic Co., 1 ♀, DeCosta, 25 July [CU]; Ocean Co., 1 ♀, Pt. Pleasant [USNM]; NEW YORK: Suffolk Co., 2 ♀♀, June-July [USNM, KVK]; Oswego Co., 1 ♀, 1 ♂, 1-5 Sept. [KVK]; MICHIGAN: Clare Co., 1 ♀, 28 June [Coll. R. R. Dreisbach]; MINNESOTA: Anoka Co., 1 ♀, 3 Aug. [Minn.]; Polk Co., 1 ♀, 6 Sept. [Minn.]; SOUTH DAKOTA: Brookings Co., 1 ♀ [MCZ]; NEBRASKA: Thomas Co., 1 ♀, Thedford, 4 July [Coll. R. R. Dreisbach]; TEXAS: Brewster Co., 3 ♂♂, The Basin, Chisos Mts., 5400 feet, July [HEE]; Presidio Co., 1 ♂, 30 May [USNM]; NEW MEXICO: Otero Co., 2 ♀♀, 1 ♂, Cloudcroft, 26 July [HEE]; Sandoval Co., 1 ♂, Jemez Springs, July [UK]; COLORADO: Boulder Co., 1 ♀, 5 ♂♂, Apr.-Aug. [USNM, MCZ]; Las Animas Co., 1 ♂, Trinidad, 10 Aug. [HEE]; Teller Co., 2 ♀♀, 1 ♂, Florissant, June [USNM, MCZ]; WYOMING: Laramie Co., 1 ♀, 6 Aug. [MCZ]; MONTANA: 2 ♀♀ (no further data) [ANSP]; Gallatin Co., 1 ♀, Bozeman, 15 June [Mass.]; ALBERTA: 1 ♀ (no further data) [CNC]; 1 ♀, Drumheller, 14 June [Alta.]; 1 ♀, Bow Island, 14 July [CNC]; YUKON: 1 ♂, Whitehorse, 3 July [CNC]; BRITISH COLUMBIA: 1 ♀, Chilcotin, 29 May [CNC]; OREGON: 1 ♀ (no further data) [USNM]; Benton Co., 2 ♀♀, 1 ♂, May, Sept. [USNM, MCZ, OSC]; CALIFORNIA: Alameda, Eldorado, Los Angeles, Mariposa, Mendocino, Monterey, Riverside, San Diego, and Shasta Cos., 6 ♀♀, 10 ♂♂, Apr.-Oct. [CAS, CIS, CU, UK, USNM].

2. **Pompilus (Ammosphex) parvulus** (Banks)

Pompiloides parvulus Banks, 1912, Jour. N. Y. Ent. Soc., 19: 227-228. [Type: ♀; Boulder Colo., 22 Aug. 1908 (S. A. Rohwer); U.S.N.M. no. 20,119.]

Psammochares (*Pompiloides*) *parvulus* Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.

Anopompilinus parvulus Dreisbach, 1950, Amer. Midl. Nat., 42: 734-735, 740, fig. 14.[7]

Pompilus (*Ammosphex*) *parvulus* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

The parameres of the male genitalia of *parvulus* distinguish it readily from *angularis* and *anomalus*; the subgenital plate is also somewhat distinctive, though subject to much individual variation. Otherwise one must rely upon more subtle characters such as the breadth of the front and the relative length of the third antennal segment as compared to the upper interocular distance. In the female there is nearly always a small amount of silvery pubescence on the lower front, and the wings are rarely as strongly violaceous as in *anomalus*.

FEMALE.—Length 8 (6-10.5) mm. Body black; wings lightly to moderately infuscated, the fore wing with a broad darker band beyond the cells; wings reflecting various colors, including violet, occasionally wholly violaceous. Pubescence very dark, rather distinctly violaceous, especially on the abdomen, on the legs often somewhat cinereous, on the sides of the lower front cinereous or somewhat silvery. Clypeus, front, vertex, temples, and prothorax with a number of erect hairs, the remainder of the body practically without erect hairs except for a few at the tip of the abdomen.

Clypeus about three times as broad as high, truncate below. Front only slightly wider than the two eyes taken together, the middle interocular distance varying from .53 to .56 (averaging .54) times the transfacial distance. Inner orbits subparallel below, converging slightly above, the upper interocular distance about .8 the lower. Postocellar line equal to or slightly greater than the ocello-ocular line. Antennae rather long and slender, the first four segments in a ratio of about 21 : 9 : 32 : 28, the third segment thus slightly longer than the first two together, and equal to from .75 to .92 times the upper interocular distance.

Propodeum rather long, with a short posterior declivity; median line feebly impressed. Spines of the tarsal comb about as long as the width of the tarsus, or slightly longer. Marginal cell of the fore wing short, removed from the wing-tip by from two to nearly three times its own length. Second and third submarginal cells much narrowed above by the arcuation of the first and third transverse cubital veins, the second transverse cubital vein erect and nearly straight.

MALE.—Length 6 (4.5-8) mm. Color black; wings subhyaline, the fore wings with a light fuscous band beyond the cells. Head, thorax, and propodeum in large part silvery-sericeous; legs silvery as far as the femora;

[7] Dreisbach designates a "lecto-holotype male" and a "lecto-allotype female" of this species, both from Boulder, Colo. [MCZ]. Banks clearly states, however, that the type of his species is in the U.S.N.M., and the female indicated above as the type is clearly marked as such.

bases of the first two or three abdominal tergites slightly silvery; pubescence of the vertex, mesonotum, scutellum, and remainder of legs and abdomen fuscous, often slightly violaceous. Temples and propleura with considerable pale erect hair; front, vertex, and pronotum with a few dark erect hairs.

Clypeus 2.5 times as broad as high, the apical margin truncate. Middle interocular distance varying from .57 to .63 times the transfacial distance; upper and lower interocular distances nearly equal. Ocelli forming an angle in front which is less than a right angle; postocellar line usually slightly greater than the ocello-ocular line. Antennae of moderate length, the first four segments in a ratio of about 11 : 5 : 12 : 12, the third segment about 2.4 times as long as thick. Postnotum about as long as the metanotum, depressed medially. Propodeum with the median line impressed, sloping very slightly for its anterior two-thirds, more steeply behind. Venation as in the female; third submarginal cell much narrowed above, sometimes triangular, rarely petiolate.

Abdominal sternite 6 with a deep U-shaped emargination. Subgenital plate tapering to a subacute or a somewhat blunt apex, the sides slightly sinuate about half-way out (Fig. 209); there is considerable variation in the shape of the plate, but it is usually broader and with less even margins than in *angularis*, and there are no prominent hairs near the base as in *anomalus*. Genitalia (Fig. 179) with the parameres clothed with short setae which are directed toward the apex (not bristling and perpendicular as in *anomalus*), the setae at the apex slightly longer. Digiti broadened and somewhat curved apically, clothed with very tiny hairs, which are absent from the extreme apex. Basal hooklets with the lower pair more strongly developed than the upper. Aedoeagus rather broad, the margins armed with short spines on the outer two-thirds.

Biology.—I have taken this species on several occasions flying close to the ground in sunny spots in forests at moderate altitudes, and also beneath trees dripping honeydew. It has been taken on the flowers of *Ceanothus fendleri, Cleome serrulata,* and *Helianthus pumilus.*

Distribution.—This form is widely distributed in the Upper Sonoran and Transition faunas of the western United States and Canada.

Specimens seen: 47 (31 ♀♀, 16 ♂♂). ALBERTA: 1 ♂, Lethbridge, 5 June [Alta.]; 1 ♂, Tilley, 7 June [CNC]; MONTANA: 1 ♀ (no further data) [ANSP]; COLORADO: Boulder Co., 3 ♀♀, 3 ♂♂, May, Aug. [MCZ, USNM]; Larimer Co., 4 ♀♀, 2 ♂♂, Poudre Canyon, 19-22 Aug. [HEE, ANSP]; Teller Co., 4 ♀♀, Florissant, June [USNM]; TEXAS: Brewster Co., 2 ♀♀, 1 ♂, The Basin, Chisos Mts., 5400 feet, 8-14 July [HEE]; NEW MEXICO: Santa Fe Co., 1 ♀, 23 Sept. [USNM]; UTAH: 1 ♂, Penrosa,

13 July [UAC]; Arizona: Cochise Co., 5 ♀♀, Carr Canyon, Huachuca Mts., 29 July [HEE]; Coconino Co, 1 ♂, Red Lake, 6450 feet, 25 July [ANSP]; 1 ♀, Bright Angel, Grand Canyon, 6880 feet, 1 Aug. [ANSP]; 1 ♀, Yavapai Pt., Grand Canyon, 18 Oct. [USNM]; 1 ♀, 1 ♂, Oak Creek Canyon, 11 Aug. [HEE]; 1 ♀, 1 ♂, Flagstaff, June, Aug. [USNM]; Pima Co., 2 ♀♀, 1 ♂, Bear Canyon, St. Catalina Mts., 7000 feet, 4 Aug. [HEE]; 2 ♂♂, Madera Canyon, Santa Rita Mts., 6500 feet, 30 July [HEE]; California: Eldorado Co., 1 ♂, Angora Peak, 26 July [CIS]; Inyo Co., 1 ♀, Whitney Portal, 6 Aug. [CIS]; Los Angeles Co., 1 ♀, San Pedro, July [ANSP]; Mariposa Co., 3 ♀♀, May [CIS].

3. **Pompilus (Ammosphex) anomalus** (Dreisbach)

Pompilus parvulus Strickland, 1947, Canad. Ent., 79: 124. [Medicine Hat, Alta.] [Based on specimens misidentified by H. E. Evans.]

Anopompilinus anomalus Dreisbach, 1950, Amer. Midl. Nat., 42: 725-726, 737, 739, figs. 1 and 2. [Type: ♂; Mountain Home Lake, Ft. Garland, Colo., 20-25 July 1932, 8300 feet; M.C.Z. no. 28,153.]

Pompilus (Ammosphex) anomalus Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934. [Erroneously placed in synonymy with *parvulus* Banks.]

This species is extremely similar to the preceding, with which it has until recently been confused. The genitalia are very similar to those of *parvulus*, but the setae along the shaft of the parameres are somewhat longer and are erect, bristling (Fig. 180); the subgenital plate is also distinctive (Fig. 210). The pubescence of the female is wholly dark and the wings strongly violaceous; the third antennal segment is about as long as the first two together, and is equal to from .6 to .8 the upper interocular distance.

Female.—Length 7.5 (6-9.5) mm. Color black, the integument in fresh specimens with a slight bluish caste, the pubescence fusco-violaceous. Front wings moderately heavily infuscated, with a broad darker marginal band, rather strongly violaceous; hind wings lightly infuscated, darker apically. Clypeus, front, vertex, front coxae, pronotum, and scutellum each with a few erect hairs; temples and propleura with fine hair; body otherwise devoid of erect hair except for some at the apex of the abdomen.

Clypeus about three times as broad as high, the apical margin truncate or very slightly arcuately concave (Fig. 234). Front rather narrow, the middle interocular distance varying from .53 to .57 (averaging .55) times the transfacial distance. Eyes converging slightly above, the upper interocular distance .8 to .9 the lower interocular. Antennae of moderate length, the first four segments in a ratio of about 25 : 10 : 35 : 30, the third segment equal to from .6 to .8 the upper interocular distance. Postocellar line equal to or slightly greater than the ocello-ocular.

Propodeum with the median line impressed. Spines of the tarsal comb from 1 to 1.5 times as long as the width of the tarsus, the one at the apex of the basitarsus about half the length of the second segment, or sometimes slightly longer. Marginal cell of the fore wing short, usually about twice as long as high, from 2.5 to 3 times its own length from the wing-tip. Second and third submarginal cells both small, much narrowed above, often nearly triangular. Third discoidal cell about 1.7 times as long as high, at least 1.5 times its own length from the outer wing margin.

MALE.—Length 6 (4.5-7) mm. Color black; wings subhyaline, broadly infuscated along the outer margin, iridescent. Pubescence of the greater part of the head, thorax, and propodeum usually silvery, basal segments of the abdomen sometimes silvery; pubescence of vertex, mesonotum, greater part of the abdomen, and sometimes much more of the body, fusco-violaceous. Front, vertex, temples, and prothorax with scattered dark hairs; remainder of body without noticeable erect hairs.

Clypeus about 2.6 times as broad as high, its apical margin slightly concave. Middle interocular distance from .56 to .62 times the transfacial distance; upper and lower interocular distances about equal. First four antennal segments in a ratio of about 11 : 5 : 10 : 12, the third segment 2.2 to 2.5 times as long as thick. Ocelli forming an acute angle in front, the postocellar line equal to or slightly greater than the ocello-ocular line. Venation much like that of the female; second and third submarginal cells small, either or both sometimes triangular; third discoidal cell short, about twice its own length from the wing margin.

Abdominal sternite 6 with a large U-shaped emargination. Subgenital plate (Fig. 210) very slender apically, inwardly abruptly broadened, with an area of rather long, suberect hairs near the sinuation of the margins. Genitalia (Fig. 180) with the parameres slightly exceeding the other appendages, the shaft with perpendicular, bristling setae of moderate length, the apex also with a few setae; disc of volsellar digitus with evenly distributed short setae; basal hooklets about equally developed; parapenials straight, short; aedoeagus very similar to that of the preceding species.

Distribution.—This species is widely distributed in the Transition and Upper Sonoran faunas of the western United States and Canada, apparently least uncommon in the coastal states.

Specimens seen: 37 (25 ♀♀, 12 ♂♂). ALBERTA: 1 ♂, Medicine Hat, 5 July [Alta.]; COLORADO: Costilla Co., 1 ♂, Ft. Garland, 8300 feet, 20-25 July [MCZ]; ARIZONA: Coconino Co., 1 ♀, Williams, 4 Nov. [UK]; Yavapai Co, 1 ♀, Prescott, 8000 feet [CAS]; BAJA CALIFORNIA: 1 ♀, San Quentin, 18 July [CAS]; CALIFORNIA: Alameda Co., 2 ♀♀, Berkeley, 27 July, 15 Sept. [USNM, CIS]; Los Angeles Co., 1 ♀ [USNM]; 1 ♀, Big Dalton Dam, 25 June [CIS]; Fresno Co., 1 ♀, Oxalis, 6 Aug. [CIS]; Marin Co., 2 ♀♀, 2 ♂♂, San Rafael [CAS]; Mariposa Co., 2 ♀♀, Yosemite, June, Aug. [UK, CIS]; Monterey Co., 1 ♀, Pacific Grove, 20 Aug.

[CAS]; Riverside Co., 1 ♀, Temecula, 4 July [CIS]; San Diego Co., 1 ♀, Alpine, 9 July [CK]; 1 ♀, Laguna Mt., 6000 feet, 23 Aug. [CAS]; 1 ♂, Borego, 8 Apr. [CIS]; San Francisco Co., 3 ♀♀, San Francisco, Sept. [CAS, USNM]; 1 ♀, 2 ♂♂, Ingleside, 25 Aug. [CU]; 3 ♀♀, 2 ♂♂, Lone Mt., 25 Apr.-4 July [CAS]; Santa Cruz Co., 1 ♀, Big Basin, 29 July [CIS]; WASHINGTON: Whatcom Co., 1 ♂, Sumas, 8 Sept. [USNM]; BRITISH COLUMBIA: 1 ♂, Crescent, 14 Aug. [CNC]; 1 ♂, Minnie Lake, 26 July [CNC]; 1 ♀, Seton Lake, Lillooet, 29 June [CNC].

Luctuosus Species-group

The members of this group are characterized in the male sex by the presence of a pencil, tuft, or series of erect hairs on the median line of the subgenital plate (very short in *solonus*). The aedoeagus is not as specialized as in the preceding group, the margins being subparallel or gradually expanded at the middle or apex of the shaft. The venation is less far removed from the outer wing margin, the marginal cell nearly always being less than twice its own length from the tip of the wing. There is a tendency toward an increased amount of erect hair on the body, and toward a greater emargination of the clypeus of the female.

4a. Pompilus (Ammosphex) solonus solonus (Banks)

Pompiloides solonus Banks, 1914, Jour. N. Y. Ent. Soc., 22: 303. [Type: ♀; Garces, Ariz., Aug. (Biederman); M.C.Z. no. 13,672.]

Psammochares (Pompiloides) solonus Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.

Anopompilinus solonus Dreisbach, 1950, Amer. Midl. Nat., 42: 735-736, 737.

Pompilus (Ammosphex) solonus Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

This species, although very similar to the preceding three by virtue of the venation and the absence of erect hair on the propodeum, is clearly a member of the *luctuosus*-group, as evidenced by the structure of the male aedoeagus, and the fact that there are some short erect setae near the apex of the subgenital plate. The integument of this form is a deep steel-blue; the front and vertex of the female are very narrow, and the third antennal segment in this sex is about the length of the upper interocular distance.

FEMALE.—Length 9 (7.5-10.5) mm. Color of integument deep blue-black, somewhat shining, the integument overlaid by a rather strongly bluish or violaceous pubescence, which is occasionally silvery on the lower front and

base of the mandibles. Fore wings fuscous, darker along the margin, strongly violaceous; hind wings subhyaline, the apex infuscated. Clypeus, front, vertex, temples, propleura, and front coxae with numerous erect hairs; pronotum, middle and hind coxae, scutellum, and sides of propodeum often with some short, sparse hair; abdominal venter and apical tergite sparsely setose.

Clypeus about three times as broad as high, its apical margin very slightly arcuately concave. Front narrow, the middle interocular distance varying from .53 to .55 times the transfacial distance. Eyes converging somewhat above, the upper interocular distance from .75 to .85 times the lower interocular. Antennae long and slender, the first four segments in a ratio of about 3 : 1 : 5 : 4, segment 3 equal to from .9 to 1.1 times the upper interocular distance. Ocelli in a right triangle on the narrow vertex; postocellar line: ocello-ocular line usually about as 5 : 4.

Pronotum somewhat full in the shoulders, its posterior margin angulate. Median line of propodeum impressed. Comb-spines of front tarsus slender, from 1.5 to 2 times as long as the width of the tarsus, the apical basitarsal spine about two thirds the length of the second tarsal segment. Longer spur of hind tibia a little over half the length of the basitarsus. Marginal cell short, about twice its own length from the wing-tip (sometimes somewhat more or less); radial vein nearly evenly arcuate. Second and third submarginal cells subequal in size and shape, both approximately as broad as high. (Wings shown in Fig. 239.)

Male.—Length 8 (6-9.5) mm. Color of integument deep steel blue; pubescence conspicuously silvery on the following parts: head except the vertex; antennal scape below; greater part of the thorax and propodeum, including the legs as far as the femora; basal bands on abdominal tergites 1 through 3 or 4; part or all of sternites 1 through 3; pubescence on the vertex, mesonotum, and remainder of abdomen fusco-violaceous. Wings subhyaline, the outer margins broadly fuscous. Temples and propleura with considerable pale hair; clypeus, front, and vertex with numerous dark hairs; pronotum and sides of propodeum sometimes inconspicuously hairy; remainder of body almost devoid of erect hairs, except the subgenital plate as described below.

Clypeus from 2.2 to 2.5 times as broad as high, its apical margin slightly concave. Middle interocular distance varying from .54 to .58 times the transfacial distance; upper interocular distance equal to or slightly greater than the lower interocular. Antennae slender, the first four segments in a ratio of about 25 : 10 : 27 : 27, segment 3 nearly three times as long as thick. Ocelli prominent; postocellar line: ocello-ocular line about as 5 : 4. Postnotum about as long as the metanotum, it and the propodeum with a well-impressed median line. Longer spur of the hind tibia slightly more than two-thirds the length of the hind basitarsus, which is very slender. Venation about as in the female.

Abdominal sternite 6 with a broadly U-shaped emargination. Subgenital plate (Fig. 217) rather broad, tapering apically to a somewhat rounded

point; disc somewhat elevated and clothed with very short erect setae, subapically with a small tuft of slightly longer setae. Genitalia (Fig. 185) with the parameres long, slightly broadened apically, coarsely and sparsely setose; parapenials stout, somewhat truncate apically; aedeagus expanded somewhat apically, its apical fifth armed along the margin with short, stout spines.

Biology.—This species is characteristic of open, sunny spots in mountain forests. A female taken by the author at Rustlers' Park, in the Chiricahua mountains of Arizona [HEE], was walking along the ground dragging an immature spider of the genus *Lycosa* [det. B. J. Kaston].

Distribution.—Typical *solonus* is an inhabitant of Transition zone forests at moderate to high elevations, ranging from Arizona and Utah west to California.

Specimens seen: 27 (20 ♀♀, 7 ♂♂). ARIZONA: Cochise Co., 1 ♀, Garces, Aug. [MCZ]; 4 ♀♀, 4 ♂♂, Huachuca Mts., June-July [HEE, CAS]; 4 ♀♀, 2 ♂♂, Chiricahua Mts., July-Aug. [HEE, UK]; 2 ♀♀, Reef, 16 Nov. [ANSP]; Coconino Co., 1 ♀, Williams, 21 July [USNM]; 1 ♀, Oak Creek Canyon, 6000 feet, 11 Aug. [HEE]; 1 ♀, Mormon Lake, 7000 feet, 12 Aug. [HEE]; Pima Co., 1 ♀, Bear Canyon, Santa Catalina Mts., 7000 feet, 4-5 Aug. [HEE]; 1 ♀, Tucson, 22 Oct. [CU]; UTAH: Cache Co., 1 ♀, Cove Fort, 14 Aug. [UK]; CALIFORNIA: Alameda Co., 1 ♀, Oakland Hills, 21 Oct. [CIS]; Marin Co., 1 ♂, Baltimore Peak, 2 July [CAS]; 1 ♀, Mt. Tamalpais, 2 July [CAS]; San Mateo Co., 1 ♀, Redwood City, 27 June [CAS].

4b. **Pompilus (Ammosphex) solonus silvivagus** new subspecies

Specimens from the eastern part of the total range of *solonus* appear to show constant differences in the male genitalia and subgenital plate, and are therefore considered to constitute a discrete subspecies. Females are more difficult to characterize, but the few specimens available to me seem to be less intensely bluish than typical *solonus*.

FEMALE (Allotype).—Length 9.5 mm.; fore wing 7 mm. Color of integument black, with vague deep metallic reflections; pubescence fusco-violaceous, on the sides of the lower front distinctly silvery. Front wings fuscous, darker apically, violaceous; hind wings subhyaline, the tip fuscous. Middle interocular distance .54 times the transfacial distance; upper interocular distance .75 times the lower interocular distance; third antennal segment equal to .95 times the upper interocular distance. Marginal cell 1.9 times its own length from the wing-tip. Other characters essentially as described under the nominate subspecies.

Three female paratypes vary in length from 7 to 10 mm., and show only minor differences from the type. The marginal cell varies from 1.8 to 2.2 times its own length from the wing-tip.

MALE (Holotype).—Length 6 mm.; fore wing 4.5 mm. Color deep blue-black; pubescence conspicuously silvery over almost the entire head, thorax, and propodeum, including the legs to the femora, as well as the bases of the first three abdominal segments; pubescence on the remainder of the abdomen darker, reflecting bluish. Wings subhyaline, the veins brownish, the fore wing with a broad fuscous band along the outer margin. Middle interocular distance .59 times the transfacial distance; inner orbits subparallel. Marginal cell of fore wing short, three times its own length from the wing-tip; second and third submarginal cells higher than wide.

Subgenital plate (Fig. 218) with the median line slightly elevated for its entire length, bearing a series of small setae, and near the apex a small tuft of slightly longer setae. Genitalia (Fig. 184) with the parameres much broadened apically, the inner margin with a series of small hairs, the upper, outer margin strongly setose. Other characters as described under the nominate subspecies.

Seven male paratypes vary in length from 7 to 9 mm. In all important essentials they agree closely with the type.

Distribution.—This form occurs east of the range of typical *solonus,* being known from Texas, New Mexico, and Colorado, with a single record from Arizona. Like *solonus solonus,* it is especially characteristic of Transition zone forests at moderate or high elevations.

Holotype.— NEW MEXICO: Otero Co., ♂, Cloudcroft, 9000 feet, 26 July 1948 (H. E. Evans) [ANSP]. *Allotype.*—Sandoval Co., N. M., ♀, Jemez Springs, 24 July 1916 (John Woodgate) [ANSP].

Paratypes.—NEW MEXICO: Otero Co., 2 ♂♂, same data as type [HEE, MCZ]; Catron Co., 1 ♀, 9 mi. W. of Quemado, 7500 feet, 14 July 1932 (Will & McIlroy) [CM]; Socorro Co., 1 ♀, Magdalena Mts., July 1904 (F. H. Snow) [UK]; ARIZONA: Pima Co., 1 ♂, Madera Canyon, Santa Rita Mts., 6500 feet, 30 July 1948 (H. E. Evans) [HEE]; COLORADO: Larimer Co., 1 ♂, Poudre Canyon, 5200 feet, 19-22 Aug. 1948 (H. E. Evans) [HEE]; Boulder Co., 1 ♀, Boulder, Sept. 1924 (T. D. A. Cockerell) [USNM]; TEXAS, 3 ♂♂ (Belfrage) [USNM].[8]

[8] Although most of Belfrage's collecting is supposed to have been done in Bosque Co., in east-central Texas, it seems to me unlikely that these specimens came from that locality. They were probably taken in the mountains of western Texas.

5a. **Pompilus (Ammosphex) michiganensis michiganensis** (Dreisbach)

Anopompilinus michiganensis Dreisbach, 1949, Ent. Amer., 29: 34, pl. I, fig. 3. [Type: ♂; Branch Co., Michigan, 31 May 1942 (R. R. Dreisbach); M.C.Z. no. 28,147.]—Dreisbach, 1950, Amer. Midl. Nat., 42: 729-730, 738, figs. 20, 24, 29, 30.

Anopompilinus aspinosus Dreisbach, 1950, Amer. Midl. Nat., 42: 730-732, 736, 738, figs. 5 and 6. [Type: ♂; Alcona Co., Michigan, 31 July (R. R. Dreisbach); M.C.Z. no. 28,151.]

Pompilus (*Ammosphex*) *michiganensis* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

This species is most closely allied to the following species, *imbecillus*, and occurs over much the same range and in much the same type of habitat. Like *imbecillus*, it has an all-black and a red-and-black subspecies, although the ranges of the subspecies of each do not coincide. *Michiganensis* may be told from *imbecillus*, in the female sex, by the absence (or nearly so) of hairs on the propodeum, and by the at most very slightly concave apical clypeal margin. The subgenital plate, with two carinae which converge posteriorly, and a subapical pencil of long hairs, can be distinguished at once from other members of the subgenus. Dreisbach's *aspinosus* appears to have been described from a male in which this pencil of setae was broken or worn off.

FEMALE.—Length 8.5 (7-10.5) mm. Color black, the first abdominal segment, except the extreme base, rufo-ferruginous, the basal half to four-fifths of the second tergite, and usually the base of the second sternite, also rufo-ferruginous. (In one specimen from Morrin, Alberta, the red is reduced to a small band on the second tergite; this specimen is probably an intergrade with subspecies *dakota*.) Wings lightly infuscated, the outer margin with a darker band. Pubescence brownish, slightly reflecting silvery on the front, propodeum, and hind coxae. Temples and propleura with considerable fine hair; clypeus, front, vertex, pronotum, scutellum, and front coxae each with a few rather strong hairs; sides of the propodeum and middle and hind coxae often with a few short, inconspicuous hairs; abdominal sternites and apical tergite slightly setose.

Clypeus about three times as broad as high, its apical margin truncate or slightly arcuately concave (Fig. 233). Front broad, the middle interocular distance about or somewhat more than .6 the transfacial distance. Eyes converging noticeably above, the upper interocular distance about .8 the lower. Ocelli in a right triangle; postocellar line equal to or slightly less than the ocello-ocular line. First four antennal segments in a ratio of about 15 : 5 : 20 : 17, segment three sometimes slightly longer or shorter than 1 plus 2, and equal to from .65 to .85 times the upper interocular distance.

Median line of propodeum impressed, but usually not strongly. Spines of the tarsal comb about as long as the width of the tarsus, or slightly longer, the apical spine on the basitarsus about half as long as the second tarsal segment. Fore wing with the marginal cell about 2.5 times as long as high, about 1.5 times its own length from the apex of the wing. Second and third submarginal cells usually slightly wider than high, the second narrowed by from one third to two thirds above, the third narrowed by at least two thirds above by the arcuation of the third transverse cubital vein, often nearly or quite triangular (Fig. 240).

MALE.—Length 7 (5-9) mm. Color black, the first and/or second abdominal tergite occasionally marked with rufous or brownish; pubescence brownish, reflecting silvery in certain lights on the propodeum, hind coxae, and front. Wings subhyaline, the outer margin of the fore wing with a broad fuscous band. Temples and propleura with fine hair; clypeus and front with scattered setae; remainder of body scarcely hairy except for the pencil of hairs on the subgenital plate.

Clypeus about 2.5 times as broad as high, its apical margin truncate. Front broad, the middle interocular distance varying from .61 to .66 times the transfacial distance. Inner orbits usually converging slightly above. Antennae elongate, the first four segments in a ratio of about 10 : 5 : 11 : 11, the third segment about three times as long as thick. Ocelli in a right triangle, the laterals about as near to each other as to the nearest eye-margin. Postnotum as long as the metanotum, impressed medially; median line of propodeum impressed, often rather weakly. Longer spur of hind tibia about three-fourths the length of the basitarsus. Venation like that of the female.

Abdominal sternite 6 with a broadly U-shaped emargination. Subgenital plate (Figs. 211, 214) with the disc somewhat elevated, the elevation bordered by two carinae which converge somewhat behind, and between which the disc is flat or somewhat concave, clothed with small setae; subapically there is a pencil of setae longer than the distance from its base to the apex of the plate; margin of the plate fringed with short setae; at the extreme base on each side is a short comb of thick, darkly pigmented setae. Genitalia (Fig. 185) with the parameres very slender, rather sparsely setose; basis volsellaris with a small group of short, thin setae; digitus with a series of clubbed setae along the inner margin, the remainder of the disc nearly devoid of setae; aedoeagus of nearly uniform breadth to the apex, which is obliquely truncate on each side, the outer apical angles with a few minute black teeth.

Biology.—This species frequents woodland glades or borders, and has been taken visiting honeydew and the flowers of *Solidago*. A male from Aweme, Manitoba [CNC], is labeled "*ex* cocoon among locust eggs".

Distribution.—This form inhabits the Hudsonian, Canadian, and Transition zones, ranging from New Brunswick, Northwest Territories, and Yukon south to Alberta, Minnesota, New York, and at high elevations to Colorado and to Georgia.

Specimens seen: 58 (25 ♀♀, 33 ♂♂). NEW BRUNSWICK: 1 ♀, Fredericton, 15 June [CNC]; QUEBEC: 1 ♂, Hemmingford, 20 June [CNC]; 1 ♂, Norway Bay, 6 July [CNC]; 2 ♂♂, Aylmer, 9 July, 11 Aug. [CNC]; ONTARIO: 1 ♂, Ottawa, 13 July [HEE]; MAINE: Lincoln Co., 1 ♀, Waldoboro, Aug. [USNM]; MASSACHUSETTS: Hampshire Co., 1 ♀, Cummington, 28 Aug. [HEE]; NEW YORK: Erie, Essex, Chautauqua, Rensselaer, Sullivan, and Tompkins Cos., 8 ♀♀, 3 ♂♂, May-Sept. [CU, MCZ, HEE, KVK]; NORTH CAROLINA: Buncombe Co., 1 ♀, Black Mt., 23 July [AMNH]; GEORGIA: Rabun Co., 1 ♂, Rabun Bald, 6 June [USNM]; INDIANA: 1 ♀ (no further data) [USNM]; MICHIGAN: Alcona, Branch, Gratiot, Ingham, and Shiawassee Cos., 1 ♀, 5 ♂♂, May-Sept. [MCZ, UK, Coll. R. R. Dreisbach, Coll. R. L. Fischer]; MINNESOTA: Bigstone, Olmstead, Ramsey, Red Lake, Traverse, Wabasha, and Washington Cos., 5 ♀♀, 3 ♂♂, May-Sept. [Minn., USNM]; COLORADO: Larimer Co., 1 ♀, Poudre Canyon, 5200 feet, 20 Aug. [HEE]; 1 ♂, Longs Peak Inn, 9000 feet, 13 July [USNM]; Grand Co., 1 ♂, Elk Creek, 7-9 July [CU]; MANITOBA: 1 ♀, Winnipeg, 19 Aug. [CNC]; 1 ♂, Aweme, 19 Mch. [CNC]; SASKATCHEWAN: 1 ♂, Great Deer, 26 May [CNC]; ALBERTA: 1 ♂, Consort, 21 June [Alta.]; 1 ♂, Edmonton, 21 May [Alta.]; 1 ♀, Morrin, 6 July [CNC]; 1 ♀, St. Paul, 22 June [Alta.]; BRITISH COLUMBIA: 4 ♂♂, Fort Nelson, 10-13 June [CNC]; YUKON: 2 ♀♀, 3 ♂♂, Watson Lake, 20-25 June [CNC]; 2 ♂♂, Snag, 24 July [CNC]; NORTHWEST TERRITORIES: 1 ♂, Norman Wells, 20 July [CNC].

5*b*. **Pompilus (Ammosphex) michiganensis dakota** (Dreisbach) new status

Anopompilinus dakota Dreisbach, 1950, Amer. Midl. Nat., 42: 728, 737, 740, figs. 9 and 10. [Type: ♂; Stump Lake, Nelson Co., No. Dak., 7 July 1920 (T. H. Hubbell); Univ. Michigan (not seen by present writer)]. —Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934. [Erroneously placed in synonymy with *michiganensis* Dreisbach.]

This form is very similar to the preceding, but the female is entirely black, and the male genitalia and subgenital plate show minor though constant differences. The range of *dakota* appears to overlap that of *michiganensis* rather broadly; because of this and because of the genitalic differences, it is possible that it should be regarded as a full species. However, in the band of overlap, *dakota* appears to occur principally at lower altitudes. Furthermore, the genitalic differences do not appear to me great enough

to outweigh the overall strong resemblance of this form to *michiganensis*.

FEMALE.—Length 8 (7-9.5) mm. Color wholly black; wings lightly to moderately infuscated, somewhat darker along the outer margin. Pubescence fuscous or somewhat cinereous, sometimes obscurely violaceous, sometimes reflecting silvery on the front, coxae, and propodeum. Third antennal segment frequently slightly longer than the first two together; spines of the tarsal comb usually slightly longer than the width of the tarsus. As in the nominate subspecies, the apical margin of the clypeus is truncate or only very slightly concave, and the propodeum has at most a trace of erect hair; these features distinguish this form from *imbecillus imbecillus*, which occurs throughout its range and often in much the same habitat.

MALE.—Length 7 (6.5-7.5) mm. Color black; pubescence either wholly dark, or a bit silvery on the front, coxae, and propodeum. Other features as described under the nominate subspecies, except for the terminalia. The subgenital plate externally is very similar to typical *michiganensis*, although in the few specimens seen the pencil of hairs appears to be slightly farther removed from the apex; internally, at the base, instead of a dense comb of stout setae on each side, are two separate groups of longer and more slender setae (Fig. 212). Genitalia (Fig. 186) with the parameres of moderate breadth, widest near the middle and tapering toward the base and apex; basis volsellaris with a large group of stout, prominent setae, some of which are clubbed; digiti elongate, the disc clothed with minute setae, the inner margin with some longer ones; aedoeagus somewhat more slender than in *michiganensis michiganensis*, the spines at the apex prominent.

Biology.—This form occurs on or near the ground in open, sunny spots in Transition Zone forests, and has also been taken on the flowers of *Heracleum lanatum*. A female from Electra Lake, Colorado [AMNH], is pinned with the spider *Thanatus formicinus* (Olivier) (Thomisidae) [det. B. J. Kaston].

Distribution.—This form inhabits the Transition fauna from Montana and North Dakota south to Arizona and New Mexico.

Specimens seen: 21 (18 ♀♀, 3 ♂♂). MONTANA: 2 ♀♀ (no further data) [ANSP]; NORTH DAKOTA: Nelson Co. (type locality; Dreisbach, 1950); COLORADO: Larimer Co., 1 ♀, Fort Collins [USNM]; 2 ♀♀, Glen Haven, 29 July [UK]; 1 ♀, Poudre Canyon, 6 Aug [MCZ]; Teller Co., 1 ♂, Florissant, 4 July [USNM]; Co. ?, 1 ♀, Electra Lake, 8400 feet, 28 June [AMNH]; NEW MEXICO: Otero Co., 2 ♀♀, 1 ♂, Cloudcroft, 9000 feet, 26 July [HEE]; 1 ♀, Sixteen Sprgs. Canyon, Sacramento Mts., 26 July [HEE]; San Miguel Co., 3 ♀♀, Beulah, July [ANSP, CU]; 1 ♀, John's Canyon, near Beulah, 4 Aug. [USNM]; ARIZONA: Coconino Co., 4 ♀♀, 1 ♂, Oak Creek Canyon, 6000 feet, 11 Aug. [HEE].

0a. **Pompilus (Ammosphex) imbecillus imbecillus** (Banks)

Anopliella imbecilla Banks, 1939, Canad. Ent., 71: 227. [Type: ♀; Colebrook, Conn., Sept. (W. M. Wheeler); M.C.Z. no. 23,475.]

Pompilus imbecillus Strickland, 1947, Canad. Ent., 79: 124. [Medicine Hat and Edmonton, Alta.]

Anopompilinus coloradensis Dreisbach, 1950, Amer. Midl. Nat., 42: 724-725, 737, 741, figs. 16 and 17. [Type: ♂; Florissant, Colo., 28 June 1908 (S. A. Rohwer); M.C.Z. no. 28,152.]

Anopompilinus banksi Dreisbach, 1950, Amer. Midl. Nat., 42: 728-729, 737, 740, figs. 11 and 12. [Type: ♂; Luce Co., Michigan, 5 July 1946 (R. R. Dreisbach); M.C.Z. no. 28,150.]

Anopompilinus imbecilla Dreisbach, 1950, Amer. Midl. Nat., 42: 736, 738, 740, figs. 13 and 15.

Pompilus (*Ammosphex*) *imbecillus* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

This species is intermediate in hairiness and in the emargination of the clypeus between the preceding and the following species. The female is best recognized by the short tarsal comb and the few long hairs on the propodeum. The subgenital plate of the male provides a ready identification character: the median line is elevated, the sides sloping roof-like from it; subapically there is a short series of erect hairs, beyond which the median line slopes rapidly to the apex. The nominate subspecies is entirely black except for the mandibles and sometimes the apical margin of the clypeus.

FEMALE.—Length 8.5 (7-10.5) mm. Color black; body clothed with a brownish or somewhat cinereous pubescence which is frequently silvery on the lower front and parts of the thorax. Wings lightly infuscated, broadly darker along the outer margin. Temples and propleura with considerable fine erect hair; clypeus, front, vertex, pronotum, scutellum, propodeum, and front coxae each with a few erect hairs; abdominal sternites and apical tergite slightly setose.

Clypeus slightly more than three times as broad as its median height, its apical margin distinctly but not deeply arcuately excised (Fig. 235). Front rather broad, the middle interocular distance varying from .57 to .61 times the transfacial distance. Eyes converging slightly above, the upper interocular distance about .85 times the lower interocular. First four antennal segments in a ratio of about 30: 10: 40: 33, the third segment equal to from .73 to .82 times the upper interocular distance. Postocellar line subequal to or slightly greater than the ocello-ocular line.

Median line of propodeum rather faintly impressed. Comb-spines of the front tarsus short, not much if any longer than the width of the tarsus, the apical basitarsal spine less than half the length of the second tarsal segment. Longer spur of the hind tibia from .55 to .67 times the length of the basitarsus; pubescence of the spurs somewhat rough, suberect, though usually less noticeably so than in *luctuosus*. Marginal cell of the fore wing usually about 1.5 times its own length from the wing-tip; second and third submarginal cells subequal in area, both about as broad as or a little broader than high, the third submarginal strongly narrowed above, often subtriangular.

MALE.—Length 7 (6-8.5) mm. Color black; wings nearly hyaline, the outer margin of the fore wing broadly infuscated. Pubescence brownish or somewhat cinereous, at least the sides of the lower front silvery, often also the clypeus, temples, and a considerable part of the thorax. Temples and propleura with considerable fine hair; front with scattered dark hairs; a few inconspicuous hairs may be present on the front coxae, pronotum, and the sides of the propodeum; abdomen without erect hairs except for a subapical tuft on the subgenital plate.

Clypeus about 2.5 times as broad as high, its apical margin slightly concave. Front rather broad, the middle interocular distance about .6 the transfacial distance. Inner orbits subparallel or diverging slightly above. First four antennal segments in a ratio of about 12 : 5 : 13 : 13, the third segment nearly three times as long as thick. Postocellar and ocello-ocular lines nearly equal. Median line of propodeum usually weakly impressed. Longer spur of hind tibia from two-thirds to three-fourths the length of the basitarsus, the latter slender and not modified as in the following species. Venation as in the female.

Subgenital plate (Fig. 213) tectiform, the sides sloping strongly from the elevated median line, subapically with a short series of prominent erect setae. Genitalia (Fig. 182) with the parameres rather slender, the ventral surface clothed rather uniformly with short setae, which may be longer along the inner margin. Volsellae with numerous rather long hairs on the basis; digitus somewhat striolate apically, the disc covered with short, clubbed setae, the apex obliquely truncate. Parapenials rather stout; aedoeagus gradually expanded toward the apex, the outer margin armed with short spines.

Biology.—The typical habitat of this species is open woodlands or woodland borders, where it may be found on the ground, logs, and low herbage. I have taken it on honeydew and on the flowers of *Ceanothus americanus*.

Distribution.—This form occurs across the continent in the Transition Zone, but appears to be absent from the Pacific states except British Columbia. It is replaced northward by subspecies *ojibwae*.

Specimens seen: 57 (41 ♀♀, 16 ♂♂). QUEBEC: 1 ♀, Aylmer, Sept. [CNC]; ONTARIO: 1 ♀, Ottawa, 20 Aug. [HEE]; MAINE: Kennebec Co., 1 ♀, Winthrop, 15 Aug. [MCZ]; NEW HAMPSHIRE: Hillsboro Co., 1 ♀, Pelham, 17 Aug. [USNM]; MASSACHUSETTS: Suffolk Co., 1 ♀, Blue Hills, Sept. [CAS]; Middlesex Co., 1 ♂, Melrose Highlands, Sept. [CAS]; CONNECTICUT: Hartford Co., 4 ♀♀, 1 ♂, 28 July 13 Sept. [HEE]; Litchfield Co., 2 ♀♀, Colebrook [MCZ]; NEW YORK: Erie, Jefferson, and Tompkins Cos., 8 ♀♀, 4 ♂♂, 19 June-4 Sept. [CU, USNM, HEE, CAS]; PENNSYLVANIA: Sullivan Co., 1 ♀, Lopez, Aug. [ANSP]; VIRGINIA: 1 ♂ (no further data) [ANSP]; MICHIGAN: Cheboygan, Huron, Lapeer, Luce, and Mecosta Cos., 4 ♀♀, 2 ♂♂, May-Aug. [MCZ, USNM, UK, coll. R. R. Dreisbach]; SOUTH DAKOTA: 1 ♀, Cedar Pass [USNM]; MONTANA: 2 ♀♀ (no further data) [ANSP]; COLORADO: 1 ♂ (no further data) [USNM]; Lake Co., 1 ♀, Leadville, 3-5 Aug. [AMNH], Larimer Co., 1 ♀, Glen Haven, Aug. [UK]; Teller Co., 1 ♀, 1 ♂, Florissant, June [MCZ, USNM]; NEW MEXICO: Otero Co., 1 ♀, 1 ♂, Cloudcroft, 9000 feet, 26 July [HEE]; ALBERTA: 3 ♀♀, 2 ♂♂, Medicine Hat, June [Alta., USNM]; 1 ♀, Edmonton, June [HEE]; BRITISH COLUMBIA: 1 ♀, Revelstoke, Selkirk Mts., June [CU]; 1 ♀, Salmon Arm, June [CNC]; 1 ♀, Trinity Valley, 29 June [CNC]; 2 ♀♀, Midday Valley, Merritt, July [CNC]; 1 ♂, Hedley, July [CNC]; 1 ♀, 1 ♂, Robson, 28 Aug., 4 Sept. [CNC].

6b. **Pompilus (Ammosphex) imbecillus ojibwae** new subspecies

This form differs from typical *imbecillus* only in having the basal segments of the abdomen marked with rufous. It thus bears considerable resemblance to *michiganensis michiganensis,* but the propodeum is somewhat hairy and the apical margin of the clypeus is distinctly excised (in the female). Named for the Ojibwa Indians of the Lake Superior region, this form occurs chiefly in the Canadian Zone, north of the range of the nominate subspecies.

FEMALE (Holotype).—Length 10 mm.; fore wing 8 mm. Color black, the abdomen marked with rufo-ferruginous on the apical two-thirds of the first tergite, all of the second tergite, a basal spot on the third tergite, all of the first sternite, and the basal half of the second sternite. Pubescence wholly brownish, except where the integument is pale. Clypeus 3.2 times as broad as high, the apical margin slightly arcuately emarginate. Middle interocular distance .59 times the transfacial distance; third antennal segment equal to .75 times the upper interocular distance. Other features as described under typical *imbecillus.*

Seventeen female paratypes vary in length from 7.5 to 10.5 mm. There is some variation in the amount of red on the abdomen; specimens from Ottawa, Ontario, Aylmer, Quebec, and Erie Co., Pa., have the red on the

abdomen considerably reduced, and probably represent intergrades with *imbecillus imbecillus*.

MALE (Allotype).—Length 7.5 mm.; fore wing 6 mm. Color black, the basal half of the second abdominal tergite and basal third of the second sternite rufo-ferruginous. Pubescence of lower front, clypeus, sides of the thorax, and propodeum somewhat silvery, elsewhere brownish. Middle interocular distance .6 the transfacial distance; upper interocular distance .93 times the lower interocular; postocellar and ocello-ocular lines about equal. Other characters, including the terminalia, not differing notably from the typical subspecies.

Two male paratypes compare closely with the type, showing minor variations in head measurements and in the amount of red on the abdomen.

Distribution.—This subspecies occurs across the continent in the Canadian and Hudsonian Zones, from New Brunswick, Ontario, Minnesota, Alberta, and British Columbia north to Northwest Territories.

Holotype.—MINNESOTA: Clearwater Co., ♀, Itasca Park, 17 July 1937 (Entomology class) [Minn.]. *Allotype.*—♂, same locality, 5 July 1943 (W. D. Murray) [Minn.].

Paratypes.—NEW BRUNSWICK: 1 ♀, Nerepis, 22 Aug. (A. G. Leavitt) [USNM]; QUEBEC: 2 ♀♀, Aylmer, 9 Aug., 1 Sept. [CNC]; ONTARIO: 1 ♀, Ottawa, 3 Aug. 1947 (W. R. M. Mason) [HEE]; 1 ♀, Sudbury, 12 July 1889 [CNC]; 1 ♂, Waubamic, 7 June 1915 [CU]; NEW HAMPSHIRE: 1 ♀ (no further data) [ANSP]; NEW YORK: Essex Co., 1 ♀, Artist's Brook, 23 June 1940 (H. Dietrich) [CU]; PENNSYLVANIA: Erie Co., 1 ♀, Cranberry Bog Trail, Presque Isle, 27 July 1933 (G. E. Wallace) [CM]; MINNESOTA: Anoka Co., 1 ♀, Republic, 30 July 1932 (C. E. Mickel) [Minn.]; Clearwater Co., 1 ♀, Lake Itasca, 27 July 1923 (S. A. Graham) [Minn.]; 1 ♂, Itasca Park, 12 June 1931, from cocoons of spotted Jack pine sawfly (L. W. Orr) [USNM]; Beltrami Co., 1 ♀, Bemidji, 19 Aug. 1922 [Minn.]; Lake Co., 1 ♀, Kawishiwi R., 30 Aug. 1919 (H. H. Knight) [Minn.]; Nicollet Co., 1 ♀, St. Peter, 27 July 1922 [Minn.]; Rock Co., 1 ♀, Luverne, 10 Sept. [Minn.]; ALBERTA: 1 ♀, Wabamun, 2 Aug. 1936 (E. H. Strickland) [Alta.]; BRITISH COLUMBIA: 1 ♀, Peace River Bridge, Taylor, 31 Aug. 1948 (W. R. M. Mason) [CNC]; NORTHWEST TERRITORIES: 1 ♀, Reindeer Depot, McKenzie Delta, 8 July 1948 [CNC].

7. **Pompilus (Ammosphex) luctuosus** Cresson

Pompilus luctuosus Cresson, 1865, Proc. Ent. Soc. Phila., 4: 452. [Lectotype: ♀; Colorado (no further data); A.N.S.P. no. 416.]—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 88.—[?]Harrington, 1896, Canad. Ent., 28: 80. [Biology.]—Dalla Torre, 1897, Cat. Hymen., VIII, p. 299.—Strickland, 1947, Canad. Ent., 79: 124. [Alta., several localities.]

[?]*Psammochares luctuosus* Banks, 1917, Bull. Mus. Comp. Zool., 61: 108. [?]Rohwer, 1917, Proc. U. S. Nat. Mus., 53: 239. [Tahoe, Calif.]

[?]*Anoplius luctuosus* Banks, 1919, Bull. Mus. Comp. Zool., 63: 233, 234. [Calif., Wash., B. C.]—[?] Cockerell, 1937, Bull. Brooklyn Ent. Soc., 32: 25. [Trail Ridge, 12000 feet, Colo.]

Anopompilinus mainensis Dreisbach, 1950, Amer. Midl. Nat., 42: 733-734, 737, 743, figs. 25 and 26. [Type: ♂; Bangor, Me., July (F. A. Eddy); M.C.Z. no. 28, 146.]

Anopompilinus hirsutus Dreisbach, 1950, Amer. Midl. Nat., 42: 733, 737, 741, figs. 18 and 19. [Type: ♂; Estes Park, Colo., 14 July 1934 (A. L. Melander); M.C.Z. no. 28,148.]

Pompilus (*Immosphex*) *luctuosus* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

A variety of species have from time to time been misidentified as *luctuosus* Cresson; unfortunately it is impossible to be sure which records are incorrect in every case, or what species was actually meant. True *luctuosus* is apparently a common species only in the Far North. The integument is dull black, not at all bluish as in the following species. In the female the clypeus is very distinctly emarginate (Fig. 236) and the longer spur of the hind tibia less than two-thirds the length of the basitarsus, the spurs rather coarsely pubescent (Fig. 224). The male is easily recognized by the modified hind basitarsus and by the characteristic subgenital plate (Fig. 215).

FEMALE.—Length 9 (7-11.5) mm. Color black, the upper outer orbits often with a very small pale spot; body clothed with a brownish, obscurely violaceous, pubescence. Fore wings moderately infuscated, darker along the outer margin, slightly violaceous; hind wings subhyaline, the apex infuscated. Body with rather abundant erect, black hairs on the mandibles, clypeus, front, vertex, temples, propleura, pronotum, front coxae, and propodeum; mesonotum, scutellum, middle and hind coxae, and usually to some extent the femora, slightly hairy; abdominal sternites and the apical tergite somewhat setose.

Clypeus about 3.3 times as broad as its median height, the anterior margin distinctly arcuately emarginate (Fig. 236). Front of moderate breadth, the middle interocular distance varying from .55 to .6 times the transfacial distance. Eyes converging slightly above, the upper interocular distance about .8 the lower. Antennae elongate, the first four segments in a ratio of about 30:10:43:35, segment 3 about .8 the upper interocular distance. Ocelli in a rather broad triangle, the postocellar line equal to or slightly greater than the ocello-ocular line. Temples rather wide, in lateral view over two-thirds the width of the eye.

Propodeum with an impressed median line and a somewhat flattened posterior declivity. Front tarsus with a comb of spines from 1 to 2.2 times as long as the thickness of the tarsus, the one at the apex of the basitarsus from one-third to two-thirds the length of the second tarsal segment. Setulae on the tibial spurs somewhat longer than the usual pubescence of the body, suberect; longer spur of the hind tibia between half and two-thirds the length of the basitarsus (Fig. 224). Marginal cell of the fore wing from 1.5 to nearly 2 times its own length from the wing-tip, the radial vein arcuate or slightly angled at the third transverse cubital vein. Second and third submarginal cells subequal in area, the second narrowed by from .3 to .6 above, the third narrowed more strongly above, often nearly triangular.

Male.—Length 8 (5.5-10.5) mm. Color black, the upper outer orbits sometimes with a small pale spot; pubescence brownish, obscurely violaceous, conspicuously silvery on the sides of the clypeus and lower front, often also to some extent on the coxae, sides of the thorax, and propodeum. Wings lightly infuscated, darker along the outer margin. Temples, occiput, and propleura with moderately dense hair; clypeus, front, and vertex rather hairy; pronotum, disc of scutellum, sides of propodeum, and front coxae with a few erect hairs; abdomen with erect hairs only on the median line of the subgenital plate.

Clypeus about 2.5 times as broad as high, the lower margin arcuately concave. Middle interocular distance varying from .57 to .61 times the transfacial distance; inner orbits subparallel or diverging slightly above. First four antennal segments in a ratio of about 12 : 5 : 11 : 12, the third segment only about 2.2 times as long as its greatest thickness. Ocelli in a rather broad triangle; postocellar line subequal to or slightly greater than the ocello-ocular line. Basal segment of the hind tarsus compressed, the inner surface with the pubescence erect, bristling. Longer spur of the hind tibia about three fourths the length of the basitarsus; spurs somewhat roughly pubescent as in the female. Venation like that of the female.

Abdominal sternite 6 broadly and shallowly emarginate. Subgenital plate (Fig. 215) nearly flat, the median line with a row of erect hairs for most of its length, these hairs longest a short distance from the apex, where they tend to form a loose tuft about as long as the distance to the apex; outer margin of the subgenital plate fringed with rather long setae. Genitalia (Fig. 188) with the parameres rather broad, fringed on the outer margin with long hairs. Digitus slightly curved, the disc clothed with short, clubbed setae. Parapenials stout, shorter than the aedoeagus, the latter rather slender, the apical fourth of the shaft with short spines along the margin.

Distribution.—This species occurs transcontinentally in the Hudsonian and Canadian Zones, sparingly entering the Transition Zone in the western states.

Specimens seen: 51 (35 ♀♀, 16 ♂♂). MAINE: 1 ♂, Bangor, July [MCZ]; QUEBEC: 2 ♂♂, Kazabazua, 9 Aug. [CNC]; MICHIGAN: Mackinaw Co., 1 ♀, 27 Aug. [Coll. R. R Dreisbach]; MINNESOTA: 1 ♀, Itasca Park, 12 May [Coll. R. R. Dreisbach]; 1 ♀, Lake Superior shore, Rosebush Township, 9 Aug. [Minn.]; SOUTH DAKOTA: 1 ♀, Cedar Pass [USNM]; DAKOTA TERR.: 2 ♀♀ (no further data) [ANSP]; WYOMING: 1 ♂, Jackson Hole, 16 Aug. [USNM]; COLORADO: 3 ♀♀ (no further data) [ANSP]; 1 ♀, Leadville, 3-5 Aug., 10,000 feet [AMNH]; 1 ♂ Estes Park, 14 July [MCZ]; 2 ♀♀, Fort Collins [USNM]; NEW MEXICO: 1 ♀, Ft. Wingate, 8 Aug. [ANSP]; IDAHO: 1 ♂, Castleford, 17 May [USNM]; CALIFORNIA: Marin Co., 1 ♀, Dillon Beach, 19 Apr. [CIS]; BRITISH COLUMBIA: 1 ♂, Chilcotin, 29 May [CNC]; 1 ♀, Windermere, 4 Aug. [Alta.]; 1 ♀, Wavenby, 11 Sept. [USNM]; 1 ♀, Lower Post, 17 June [CNC]; 2 ♂♂, Fort Nelson, 6 June [CNC]; ALBERTA: 3 ♀♀, 1 ♂, Medicine Hat, 15 June, 20 Aug. [CNC, Alta., USNM]; 1 ♀, Lethbridge, 28 Aug. [CNC]; 1 ♂, Drumheller, 14 June [Alta.]; 1 ♂, Edmonton, 13 May [Alta.]; YUKON: 4 ♀♀, 1 ♂, Whitehorse, 3 July-1 Aug. [CNC]; 1 ♀, 1 ♂, Watson Lake, 17-24 June [CNC]; NORTHWEST TERRITORIES: 8 ♀♀, 1 ♂, Reindeer Depot, MacKenzie Delta, 12 July-13 Aug. [CNC]; 1 ♀, 1 ♂, Norman Wells, 12-23 Aug. [CNC].

8. **Pompilus (Ammosphex) occidentalis** (Dreisbach)

Anopompilinus occidentalis Dreisbach, 1950, Amer. Midl. Nat., 42: 726-728, 736, 738, 743, figs. 27 and 28. [Type: ♂; Pinecrest, Tuolumne Co., Calif., 29 July 1947 (P. H. Arnaud); M.C.Z. no. 28,149.]

Pompilus (*Ammosphex*) *occidentalis* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 934.

This not uncommon inhabitant of the western United States and Canada has apparently escaped detection until recently because of its close similarity to *luctuosus* Cresson, from which the characters presented in the keys serve to separate it. The integument has a distinct bluish caste, particularly apparent on the front. In this species the spininess of the male aedoeagus reaches its ultimate development, this structure suggesting a machinist's file.

FEMALE.—Length 8.5 (7-10) mm. Color black, the integument faintly reflecting deep steel-blue, especially on the front, the upper, outer orbits often with a small pale spot. Wings moderately infuscated, somewhat darker apically, violaceous. Pubescence brownish-fuscous, somewhat violaceous, nowhere silvery. Body with erect black hairs as follows: mandibles, clypeus, front, vertex, pro- and mesonota, disc of scutellum, propodeum, and coxae, conspicuously though rather sparsely; temples, occiput, and propleura more densely but with finer hairs; abdominal venter and apical tergite sparsely setose.

Clypeus about three times as broad as high, its apical margin broadly and not deeply emarginate. Front of moderate breadth, the middle interocular distance varying from .54 to .6 times the transfacial distance. Eyes somewhat convergent above, the upper interocular distance about .85 times the lower interocular. Antennae rather elongate, the first four segments in a ratio of about 30 : 10 : 42 : 35, the third segment equal to about .8 the upper interocular distance. Ocelli in approximately a right triangle, the postocellar and ocello-ocular lines about equal. Temples moderately developed, in lateral view at least half the width of the eye.

Propodeum with an impressed median line. Comb-spines of front tarsus slender, nearly twice as long as the width of the tarsus, the one at the apex of the basitarsus about two-thirds the length of the second tarsal segment, or somewhat longer. Longer spur of the hind tibia from .67 to .8 times the length of the basitarsus, the spurs and the basitarsus more slender than in *luctuosus*, the pubescence on the spurs fine and appressed (Fig. 225). Marginal cell short, about 1.5 times its own length from the wing-tip; radial vein nearly evenly arcuate. Second and third submarginal cells each strongly narrowed above.

MALE.—Length 7 (5-9) mm. Color black, the integument faintly reflecting deep steel-blue. Pubescence fusco-violaceous, reflecting silvery on the clypeus, lower front, and often also on the greater part of the coxae, mesopleura, and propodeum. Wings lightly infuscated, the outer margin broadly darker; wings iridescent, faintly violaceous. Clypeus, front, vertex, anterior coxae, pronotum, and propodeum with numerous erect hairs; temples and propleura with denser, finer hair; venter with a few sparse, short setae, and a long pencil of hairs on the subgenital plate.

Clypeus about 2.5 times as broad as high, the lower margin slightly arcuately concave. Front of moderate breadth, the middle interocular distance about .6 the transfacial distance. Upper interocular distance subequal to or slightly greater than the lower interocular. Antennae slender, the first four segments in a ratio of about 22 : 10 : 25 : 25, segment 3 about 2.5 times as long as its greatest thickness. Postnotum dorsally nearly as long as the metanotum, its median line and that of the propodeum distinctly impressed. Longer spur of the hind tibia about three-fourths the length of the basitarsus, the latter unmodified. Venation like that of the female, the cells often a bit farther removed from the outer wing margin.

Abdominal sternite 6 with a broad, U-shaped emargination. Subgenital plate (Fig. 216) nearly flat, the apex rounded, the disc with a subapical pencil of long setae, at least twice as long as the distance from its base to the apex of the plate. Genitalia (Fig. 187) with very broad parameres, which much exceed the other appendages in length; digitus striolate apically, clothed with small, clubbed setae; parapenials short, slender, curved; aedoeagus somewhat broadly lanceolate, the apex truncate, the margins for the apical half or more beset with stout, dark spines of varying size.

Distribution.—This species is an inhabitant of mountain forests of the West, apparently chiefly in the Transition Zone, ranging from Alberta and British Columbia south at high altitudes to New Mexico, Arizona, and California.

Specimens seen: 44 (24 ♀♀, 20 ♂♂). ALBERTA: 1 ♂, Banff, 1 July [USNM]; 1 ♂, Medicine Hat, 3 June [Alta.]; MONTANA: 2 ♀♀, 1 ♂ (no further data) [ANSP]; Dawson Co., 1 ♀, Glendive, 11 June [USNM]; COLORADO: 3 ♀♀ (no further data) [USNM]; Adams Co., 1 ♂, Bennett, 12 Aug. [UK]; Costilla Co., 1 ♀, Ft. Garland, Mt. Home, 8300 feet, July [MCZ]; Boulder Co., 2 ♀♀ [USNM]; Mineral Co., 2 ♀♀, Creede, 8844 feet, Aug. [UK]; NEW MEXICO: Otero Co., 1 ♀, 4 ♂♂, Sacramento Mts., 8000-9000 feet, June-July [HEE, UK]; ARIZONA: Cochise Co., 1 ♂, Chiricahua Mts., Rustler's Park, July [UK]; Pima Co., 1 ♀, Mt. Lemmon, Santa Catalina Mts., Aug. [HEE]; NEVADA: Elko Co., 1 ♀, Talbot Creek, Lamoille, 23 July [MCZ]; CALIFORNIA: Inyo Co., 1 ♂, Bishop, 28 July [UK]; 1 ♂, Glacier Lodge, Big Pine Creek, 8000-11000 feet, Aug. [CAS]; Monterey Co., 4 ♀♀, 1 ♂, Carmel, May-Oct. [CAS]; San Bernardino Co., 1 ♀, Big Bear, 13 Aug. [HEE]; Tulare Co., 1 ♀, Dorst Camp, 23 July [CIS]; Tuolumne Co., 1 ♂, Pinecrest, 29 July [MCZ]; OREGON: Deschutes Co., 1 ♂, Sunshine Shelter, 16 Aug. [OSC]; Hood River Co., 1 ♂, Mt. Hood, 3000-6000 feet, 5 Aug. [CAS]; Marion Co., 1 ♀, Silver Creek Park, 10 Aug. [OSC]; Washington Co., 1 ♂, Forest Grove, 1 June [OSC]; WASHINGTON: Mt. Rainier Nat. Park, 1 ♂, Paradise Valley, July [CAS]; Pierce Co., 1 ♀, Buckley, 6 July [UK]; BRITISH COLUMBIA: 1 ♀, Keremeos, 28 June [CNC], 1 ♀, Midday Valley, Merritt, 10 July [CNC]; 1 ♂, Okanagan, Aug. [CNC]; 2 ♂♂, Robson, 19 Aug., 14 Sept. [CNC].

F. Subgenus **ARACHNOSPILA** Kincaid

Arachnospila Kincaid, 1900, Proc. Wash. Acad. Sci., 2: 509. [Type: *Arachnospila septentrionalis* Kincaid, 1900 (= *fumipennis fumipennis* Zetterstedt, 1838); monobasic.]—Pate, 1946, Trans. Amer. Ent. Soc., 72: 74.—Evans, 1951, U. S Dept. Agri., Monogr. 2, p. 934.

Pycnopompilus Ashmead, 1902, Canad. Ent., 34: 83. [Type: *Pompilus scelestus* Cresson, 1865; original designation.]—Pate, 1946, Trans. Amer. Ent. Soc., 72: 75, 105. [Present synonymy indicated.]—Banks, 1947, Bull. Mus. Comp. Zool., 99: 422-423. [South American species.]—Dreisbach, 1949, Ent. Amer., 29: 8, 11, 34, pl. I, fig. 4.

Arachnophila Ashmead, 1902, Proc. Wash. Acad. Sci., 4: 134. [*Nec* Ashmead, 1902, Canad. Ent., 34: 86.]

Psammochares (*Psammochares*) *Fumipennis*-group Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, pp. 154, 162, and 195.

Ammosphex Wilcke, 1942, Ent. Berichten, 11: 25. [In part.]—Wilcke, 1943, Overdr. uit Med. Landbouwhoogeschool Wageningen, 47: 47-61. [In part.]

This subgenus is closely related to the preceding, but the venation extends farther toward the outer wing margin, the marginal cell being approximately its own length from the wing-tip and the third discoidal cell about or less than its own length from the outer wing margin (Fig. 241). The tarsal comb of the female is strongly developed; the body is generally more strongly hairy than in *Ammosphex*. The last segment of the front tarsus of the male (Fig. 230) is shaped as in *Anoplochares*, not as in *Ammosphex;* the male genitalia are very characteristic.

Subgeneric characters.—Small to fairly large wasps, 7 to 20 mm. in length. Color wholly black, or the basal abdominal segments marked with rufous. Front with rather dense erect, dark hair; temples and propleura with abundant dark hair; pronotum and propodeum with a considerable amount of erect hair; venter and apical segments of the female with numerous dark setae. Mandibles bidentate in the female, unidentate in the male. Labrum exserted only a short distance or not at all beyond the clypeus. Malar space wanting. Antennae elongate, the third segment in the male always well over twice as long as thick.

Pronotum strongly angulate behind. Postnotum half or more the length of the metanotum and more or less transversely striate. Front tarsus of female with a well-developed comb, the spines from one to three times as long as the width of the tarsus, the basitarsus with from 3 to 5 comb-spines. Apical tarsal segments of the female with a row of median spines beneath, and usually some lateral spines as well. Last segment of front tarsus of male produced on the inner margin, but less strongly than in *Ammosphex*, the segment widest about two-thirds the distance from the base; both claws of this segment are bifid, the inner one with the inner ray longer than in *Ammosphex* (Fig. 230). Pulvillar comb of about 13-15 setulae in the female (Fig 232). Wing venation as shown in Fig. 241, showing little variation in the subgenus. Marginal cell long, about three times as long as high, the radial vein nearly evenly arcuate; this cell is not more than 1.2 times its own length from the wing-tip, usually about equal to it. Second and third submarginal cells both four-sided and fairly wide above. Third discoidal cell about or slightly less than its own length from the outer wing margin.

Abdomen of the male relatively stout; subgenital plate with the disc slightly to strongly elevated, not as slender as in the following subgenus, nor produced on each side internally as in that group. Genitalia with the basal hooklets double; aedoeagus simple and unarmed. Digiti more or less rounded apically and provided here with several upright setae; inner margin more or less arcuately excised toward the base, the upper end of the excision angulate. Parameres strong, setose, of variable breadth.

Biology.—The species of this subgenus are hunters of errant spiders and are not highly selective of their prey. The nest is a short tunnel in sand or soft earth with a single terminal cell. Our three species are all fairly common, and a few notes regarding their biology are included under each.

Distribution.—Holarctic; represented in the Palaearctic Region by *fumipennis* Zetterstedt and *rufus* Haupt. The former occurs in northern North America as well as in northern Eurasia; the latter, Haupt's *rufus*, appears to be no more than subspecifically distinct from the North American *scelestus* Cresson. Banks (1947) has assigned two South American species to this group. Although 14 names are available for the Nearctic species, there appear to me to be but three highly variable, widely distributed species in our fauna.

Key to Species

Females

1. Scape not hairy; apical margin of clypeus somewhat arcuately excised; postocellar line less than the ocello-ocular line, the ocelli in rather a small triangle, the front angle of which is usually about a right angle. 1. **arctus** Cresson

   Scape with a number of hairs below or on the sides which are usually about as long as the thickness of the scape; apical margin of clypeus truncate or very slightly arcuately concave; ocelli variable 2

2. Ocelli forming a right or obtuse angle in front, the post-ocellar line less than the ocello-ocular line; front basitarsus with from 3 to 5, most commonly 4, comb-spines; body black, usually noticeably reflecting bluish .....2. **scelestus** Cresson

   Ocelli forming an acute angle in front, the postocellar and ocello-ocular lines about equal; front basitarsus with three comb-spines; body black, slightly violaceous, or black and red 3

3. Base of the abdomen rufous; pubescence brownish, often somewhat silvery on the hind coxae .....3*a*. **fumipennis fumipennis** Zetterstedt

   Wholly black; pubescence very dark, somewhat violaceous. 3*b*. **fumipennis eureka** (Banks)

Males

1. Subgenital plate merely convexly raised medially, toward the base with a pair of elevations (usually rounded, though sometimes acute, and sometimes obsolescent) (Fig. 221); parameres of genitalia slender throughout (Fig. 191) .....1. **arctus** Cresson

Subgenital plate keeled, the median line strongly and sharply elevated; parameres much broadened apically 2

2. Median elevation of subgenital plate sloping evenly from front to rear, the posterior slope convex or nearly straight (Fig. 219); digiti strongly spatulate (Fig. 190) .....2. **scelestus** Cresson

Median elevation of subgenital plate abruptly declivous behind, the posterior slope concave (Fig. 220); digiti less strongly enlarged apically (Fig. 189) 3

3. Base of the abdomen marked with rufous; pubescence brownish, often in part silvery .....3*a*. **fumipennis fumipennis** Zetterstedt

Wholly black; pubescence very dark, somewhat violaceous, sometimes silvery on the lower front .....3*b*. **fumipennis eureka** (Banks)

1. Pompilus (Arachnospila) arctus Cresson

Pompilus arctus Cresson, 1865, Proc. Ent. Soc. Phila., 4: 453. [Type: ♂; Colorado (no further data); A.N.S.P. no. 554.]—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 92.—Packard, 1874, Guide to the Study of Insects, p. 273.—Dalla Torre, 1897, Cat. Hymen., VIII, p. 273.—Strickland, 1947, Canad. Ent., 79: 124. [Edmonton, Alta.]

Psammochares anoplinus Banks, 1919, Bull. Mus. Comp. Zool., 63: 231-232. [Type: ♀; Medicine L. to Jasper, Alta., 4 July 1915 (J. C. Bradley); C.U. no. 683.]

Pycnopompilus siouxensis Dreisbach, 1950, Amer. Midl. Nat., 43: 592, 593, 598, figs. 46 and 47. [Type: ♂; Glen, Sioux Co., Nebr., 4000 feet, 13 Aug. 1906; Univ. Nebraska.][9] New synonymy.

Pycnopompilus sculleni Dreisbach, 1950, Amer. Midl. Nat., 43: 587, 594, 598, figs. 33 and 37. [Type: ♂; Cornucopia, Ore., 7100 feet, 25 July 1936 (H. A. Scullen); M.C.Z. no. 28,382.] New synonymy.

Pycnopompilus arctus Dreisbach, 1950, Amer. Midl. Nat., 43: 593, 595, 598, fig. 45.

Pycnopompilus eureka Dreisbach, 1950, Amer. Midl. Nat., 43: 587, 596, 598, figs. 34 and 38. [*Nec* Banks, 1919; misidentification.]

Pycnopompilus luctuosus Dreisbach, 1950, Amer. Midl. Nat., 43: 593, 597, 598, figs. 43 and 44. [*Nec* Cresson, 1865; misidentification.]

Pompilus (*Arachnospila*) *arctus* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

The species of *Arachnospila* have been much confused in the past, and *arctus,* in particular, has rarely been correctly identified. The tarsal comb, usually a reliable diagnostic character in the Pompilini, varies in the number of spines and in their length in both *arctus* and *scelestus,* so that this cannot be used to separate

[9] At this writing, this type had not yet been deposited at this institution, and I have not seen it.

these species. Although all three species of this subgenus show considerable variation in the amount of erect hair on the body, the antennal scape in *arctus* is devoid of erect hairs, but not so in the other two species. This character may seem tenuous enough, but it seems perfectly reliable in identifying *arctus*. In addition certain other characters, especially the slight emargination of the clypeus of the female (not unlike that of *imbecillus*, shown in Fig. 235), and the male genitalia, serve to identify this species.

The male subgenital plate of this species (Fig. 221) is also highly characteristic, although subject to much individual variation, as described below. Dreisbach (1950) has recently applied five names to this species, based solely on very minor differences in the subgenital plate. There is nothing else to support this division of the species, and with a sufficient series of males before him one is easily convinced that intraspecific variation readily accounts for Dreisbach's five "species", and for as many other variants as one might wish to select.

FEMALE.—Length 11 (7.5-14.5) mm. Color black, the upper posterior orbits usually with a very slender pale streak. Fore wings moderately infuscated, darker along the margin, usually somewhat violaceous; hind wings lightly infuscated, darker apically. Pubescence fuscous, obscurely reflecting deep bluish or violet (specimens from the Pacific states sometimes rather strongly bluish). Antennal scape without erect hairs; clypeus, front, vertex, and temples varying from slightly to rather densely hairy; pronotum and front coxae somewhat hairy; propodeum with considerable erect hair; remainder of thoracic dorsum and pleura, front femora, and middle and hind coxae often somewhat hairy; abdominal venter and apical tergite setose.

Clypeus about 3 times as broad as high, the apical margin distinctly though shallowly concave. Front broad, the middle interocular distance about .6 the transfacial distance, or somewhat more. Inner orbits converging slightly above, the upper interocular distance about .8 the lower. Ocelli forming an angle in front which is usually less than a right angle; postocellar line less than the ocello-ocular line as 3:4, rarely approaching 1:1. Antennae elongate, the first four segments in a ratio of about 30:10:45:38, though this ratio rather variable, segment 3 sometimes not exceeding the first two together; third segment equal to from .6 to 1.0 times the upper interocular distance, this factor varying with the size of the specimen.

Propodeum with the median line impressed in front; slope rather even, slightly steepened behind. Tarsal comb variable, the basitarsus with either 3 or 4 spines, the spines varying in length from 1 to 3 times the width of the tarsal segments. Wing venation not differing notably from that of *scelestus*, shown in Fig. 241; the third submarginal cell is frequently slightly larger in area than the second.

MALE.—Length 8.5 (6.5-12) mm. Color black, the outer orbits usually with a very slender pale spot, the inner orbits sometimes also with such a spot. Wings lightly infuscated or nearly hyaline, broadly darker along the outer margin. Pubescence dark, often somewhat violaceous, that of the sides of the lower front more coarse and nearly always conspicuously silvery; silvery pubescence sometimes more extensive, especially in eastern specimens, often involving the coxae, sides of the thorax, and the propodeum. Body with a variable amount of erect hair, the scape always without erect hair, the propodeum always somewhat hairy.

Clypeus from 2.3 to 2.5 times as broad as high, the apical margin slightly concave. Front broad, the middle interocular distance varying from .6 to .64 times the transfacial distance. Inner orbits converging slightly above; ocelli forming a right or acute angle in front, the postocellar line usually less than the ocello-ocular line. First four antennal segments in a ratio of about 3 : 1 : 3 : 3, or the third segment proportionally slightly longer. Median line of the propodeum impressed. Longer spur of the hind tibia about .7 the length of the basitarsus. Venation as in the female.

Abdominal sternite 6 with a broad U-shaped emargination. Subgenital plate (Fig. 221) rather broad, the disc convexly elevated medially, with an elevation on each side near the base; these basal elevations are usually rounded and not prominent, as in the figure, but they are occasionally produced as sharp tubercles. Genitalia (Fig. 191) with the parameres slender throughout, somewhat setose, with a hyaline area along the inner margin. Digiti somewhat variable in shape, the apex with several prominent setae, the inner margin excised below, the appendage as a whole somewhat suggesting the head of a cockatoo. Parapenials stout and straight, closely embracing the slightly longer aedoeagus.

Biology.—One of the more common species of *Pompilus* within its range, *arctus* is most often encountered on or near the ground in open wooded areas or in parks, where it nests in soft earth. The three records of its prey known to me are as follows: (1) a specimen from Aweme, Manitoba [CNC] taken with an immature female *Arctosa* sp. (Lycosidae); (2) a specimen taken by W. R. M. Mason at Edmonton, Alberta [CNC] with an immature *Clubiona* sp. (Clubionidae); (3) a specimen in the author's collection taken at Syracuse, New York, by Mr. Howard Miller of that city, with a female *Amaurobius ferox* Walck. (Amaurobiidae) [determinations by B. J. Kaston].

Mr. Miller has provided me with the following notes pertaining to the last of these records. The wasp was encountered in a residential part of the city, dragging the spider across the grass of a lawn. The wasp walked backward, carrying the spider head-up,

grasping it by the coxae. After it had traveled about 15 feet, the wasp reached the edge of a side walk, where the soil was somewhat gravelly, and where it entered a previously prepared burrow in the earth. The hole was about three inches deep, straight and diagonal. The spider was taken into the laboratory, where it remained torpid but alive for 12 days. On the thirteenth day it would no longer respond to stimuli, and on the fourteenth day it showed signs of decomposition.

Distribution. This species ranges transcontinentally in the Hudsonian, Canadian, and Transition Zones.

Specimens seen: 418 (222 ♀♀, 196 ♂♂). The following are marginal records: Nova Scotia: Cape Breton Isl., 1 ♀, Baddeck, Aug. [MCZ]; Quebec: Anticosti Isl., 1 ♀, 6 Aug. [CNC]; Labrador: 1 ♂, Goose Bay, 14 Aug. [CNC]; Northwest Territories: 1 ♀, Crow's Nest Pass, 1888 [CNC]: 1 ♀, Fort Norman, 6 Aug. [CNC]; Yukon: 3 ♂♂, Whitehorse, July, Aug. [CNC]; 2 ♂♂, Watson Lake, 24 June [CNC]; British Columbia: Vancouver Isl., 1 ♀, Victoria [CNC]; California: Riverside Co., 1 ♀, Tahquitz Valley, San Jacinto Mts., 14 June [CAS]; San Bernardino Co., 1 ♀, Oak Glen Lodge, 5000 feet, July [CAS]; Arizona: Cochise Co., 2 ♂♂, Chiricahua Mts., 8000 feet, 29 June [CAS]; New Mexico: Otero Co., 3 ♀♀, 1 ♂, Cloudcroft, 9000 feet, 26 July [HEE]; Colorado: Teller Co., 1 ♀ 3 ♂♂, Florissant, June-July [USNM]; Nebraska: Madison Co., 1 ♀, Meadow Grove, June [USNM]; Iowa: Webster Co., 1 ♀, 20 June [USNM]; Ohio: Franklin Co., 1 ♂, 12 July [RWS]; West Virginia: Randolph Co., 1 ♀, 1 ♂, Cheat Mt., 2000 feet, June [CM]; District of Columbia: 6 ♀♀, 5 ♂♂, Washington, 29 May-8 Sept. [MSV, USNM].

2. **Pompilus (Arachnospila) scelestus** Cresson

Pompilus scelestus Cresson, 1865, Proc. Ent. Soc. Phila., 4: 451. [Lectotype: ♀; Colorado (no further data); A.N.S.P. no. 415.]—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 88. [Conn. N. J.]—Cresson, 1872, Trans. Amer. Ent. Soc., 4: 203. [Texas.]—Provancher, 1882, Nat. Canad., 13: 35-36. [Que.]—Dalla Torre, 1897, Cat. Hymen., VIII, p. 321.—Peckham and Peckham, 1898, Wisc. Geol. Nat. Hist. Survey Bull. no. 2, p. 153. [Biology.]—Peckham and Peckham, 1905, Wasps Social and Solitary, pp. 230-243. [Biology.]—Strickland, 1947, Canad. Ent., 79: 124. [Alta.]

Pycnopompilus scelestus Ashmead, 1902, Canad. Ent., 24: 83. [Selected genotype of n. gen. *Pycnopompilus*.]—Dreisbach, 1950, Amer. Midl. Nat., 43: 593, 597, 599, figs. 36 and 41.

Psammochares astur Banks, 1912, Jour. N. Y. Ent. Soc., 19: 225. [Type: ♀; Great Falls, Md., 12 July (N. Banks); M.C.Z. no. 13,688.]—Banks,

1917, Bull. Mus. Comp. Zool., 61: 108.—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 986.—Brimley, 1936, Jour. Elisha Mitchell Sci. Soc., 52: 128-129. [N. C.]—Procter, 1938, Biol. Survey Mt. Desert Reg., VI, Insecta, p. 430. [Me.]

Psammochares scelestus Rohwer, 1916, Conn. Geol. Nat. Hist. Survey, Bull. 22, p. 633.—Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.—Rau and Rau, 1918, Wasp Studies Afield, pp. 64-67. [Biology.]—Banks, 1919, Bull. Mus. Comp. Zool., 63: 233. [Calif., Wash.]—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 986.—Brimley, 1936, Jour. Elisha Mitchell Sci. Soc., 52: 128-129.

Psammochares sublaevis Banks, 1921, Ann. Ent. Soc. Amer., 14: 20. [Type: ♀; Marion Co., Ind. (H. Morrison); M.C.Z. no. 13,693.]—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 986.

Pycnopompilus subscelestus Dreisbach, 1950, Amer. Midl. Nat., 43: 591-593, 599, figs. 39 and 40. [Type: ♂; Ute Creek, Colo., 30 July (R. W. Dawson); Univ. Nebraska.][10] New synonymy.

Pycnopompilus astur Dreisbach, 1950, Amer. Midl. Nat., 43: 595.

Pycnopompilus sublaevis Dreisbach, 1950, Amer. Midl. Nat., 43: 598.

Pompilus (*Arachnospila*) *scelestus* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

This is the best known and possibly the most common species of *Pompilus* in our fauna. The male is easily recognized by the characteristic subgenital plate (Fig. 219). The female closely resembles the preceding species; however, the scape is hairy, generally rather prominently so, the clypeus is scarcely concave apically, and the ocellar triangle is rather flat, the front angle generally being a right angle or greater. Like *arctus,* this is a very variable species; the range of variation in size is possibly the greatest of any of the Pompilini. The smallest female seen by the writer was 6.5 mm. long, the largest 20 mm. long!

FEMALE.—Length 13.5 (6.5-20) mm. Color black, the upper posterior orbits with a slender pale spot. Pubescence dark, more or less conspicuously reflecting deep steel blue, less apparent and fading to purplish in older specimens. Fore wings fuscous, darker in a band along the margin, in fresh specimens strongly violaceous; hind wings lightly infuscated, darker apically. Scape with at least a few hairs below or on the sides which are about as long as the thickness of the scape; clypeus, front, vertex, temples, and propleura all with considerable erect hair; propodeum hairy over its entire surface; pronotum, mesonotum, scutellum, metanotum, pleura, coxae, and to

[10] At this writing, this type had not been deposited at the institution stated, and I have not seen it.

some extent the femora, with a variable amount of short, erect hair; venter and apical tergite setose.

Clypeus from 2.6 to 3 times as broad as high, its apical margin truncate or very slightly incurved medially. Front broad, the middle interocular distance usually about .6 the transfacial distance. Inner orbits convergent above, the upper interocular distance equal to from .75 to .83 times the lower interocular distance. Ocelli in a somewhat flattened triangle, the front angle a right angle or somewhat greater; ocello-ocular line nearly always distinctly greater than the postocellar line. First four antennal segments in a ratio of about 3 : 1 : 5 : 4, though somewhat variable in this respect, the third segment equal to from .75 to 1.0 times the upper interocular distance.

Median line of the propodeum at most slightly impressed. Front tarsus with a well-developed comb, the spines varying from 1.5 to 3 times as long as the thickness of the tarsus, the basitarsus with 3 or 4 (rarely 5) comb-spines. Venation as shown in Fig. 241 and described under the subgeneric heading; second and third submarginal cells subequal in area.

Male.—Length 11.5 (6-16) mm. Color black, the upper outer and middle inner orbits usually with a very small pale spot. Pubescence fusco-violaceous, on the sides of the lower front often silvery. Wings lightly to rather heavily infuscated, darker along the outer margin, iridescent or violaceous. Scape hairy below; clypeus, front, vertex, temples, and propleura generally rather densely hairy; thoracic dorsum and pleura, propodeum, front coxae, and base of the first abdominal tergite usually with considerable erect hair.

Clypeus about 2.5 times as broad as high, its apical margin truncate or slightly concave. Middle interocular distance about .6 the transfacial distance; upper interocular distance about .9 the lower interocular. Ocelli in a flattened triangle, the front angle usually a right angle or greater; ocello-ocular line distinctly greater than the postocellar line. Antennae elongate, the first four segments in a ratio of about 15 : 5 : 16 : 15. Median line of the propodeum feebly if at all impressed. Longer spur of hind tibia about two-thirds the length of the basitarsus.

Abdominal sternite 6 with a deep U-shaped emargination. Subgenital plate (Fig. 219) strongly keeled, the keel in profile rather evenly arcuate from front to rear, or the posterior slope nearly straight. Genitalia (Fig. 190) with the parameres much broadened apically, their inner margin with a rather large membranous and unpigmented area, the outer margin with numerous long setae. Digiti capitate, larger apically than in the other members of this subgenus, the disc densely clothed with setae which are longest at the lower inner angles. Parapenials slender and nearly straight; aedoeagus simple, somewhat expanded apically.

Biology.—This is a wide-ranging species, occurring in a variety of habitats, including sand dunes, fields, gardens, and open woodlands. It has been taken on the flowers of *Astragalus, Petalostemon, Sphaeralcea, Solidago,* and *Daucus carota.* The nesting

habits have been studied and described by the Peckhams (1898 and 1905) and the Raus (1918). The recorded hosts are as follows: (1) a Lycosid spider (Peckhams), (2) *Dolomedes* sp. (Pisauridae) (Raus). To this I am able to add the following: (3) a specimen taken at Logan, Utah [MCZ], with a young *Phidippus* sp. (Salticidae), and (4) a specimen taken by the author at East Hartford, Conn., with a male *Lycosa gulosa* Walck. (Lycosidae) [det. B. J. Kaston].

The nest of this species is constructed in sand or soft earth, and is oblique and about 3 or 4 inches deep; it is apparently prepared before the search for the spider begins, although it may be enlarged afterward to fit the size of the spider. The wide variety of spiders preyed upon by this species doubtless explains its great range in size. After the spider is placed in the cell, the egg is laid transversely beneath the abdomen. The Raus remark upon the fact that spiders taken by this wasp are often so severely stung that they show no signs of reviving for several days. My own experience has been just the opposite. The *Lycosa gulosa* mentioned above recovered completely within two hours and ran actively around the container in which I had placed it; in spite of this the egg of the wasp hatched in three days and the larva developed normally, reaching a large size in four days, when it died. In the confines of the nest this activity of the spider would of course have been impossible. *P. scelestus* is apparently parasitized by *Ceropales*, and in a different manner by *Evagetes parvus* (*Pompilus subviolaceus* of the Peckhams, 1905). For further details on the behavior of this species, the reader is referred to the excellent accounts by the Peckhams and the Raus.

Distribution.—Transcontinental in the Upper Austral and Transition Zones, entering the Canadian Zone to a limited extent, especially in the West.

Specimens seen: 375 (212 ♀♀, 163 ♂♂). The following records are selected from periphery of the range: Nova Scotia: 1 ♂, Kentville, July [CNC]; New Brunswick: 1 ♂, Fredericton, June [CNC]; Quebec: 1 ♂, Duchesney, 4 Aug. [CU]; Ontario: 1 ♀, Toronto, 1 July [CNC]; Michigan: Cheboygan Co., 3 ♀♀, 3 ♂♂, June-July [MCZ, CIS]; Minnesota: Clearwater Co., 2 ♀♀, 1 ♂, Itasca Park, June-July [Minn.]; Manitoba: 1 ♀, 1 ♂, Aweme, July-Sept. [CNC]; Alberta: 1 ♂, Edgerton, 20 June [Alta.]; British Columbia: 2 ♂♂, Taylor, 3 June [CNC];

California: Los Angeles Co., 1 ♀, Mt. San Antonio, 5 Aug. [CIS]; Arizona: Cochise Co., 1 ♀, Huachuca Mts., 15 June [CAS]; New Mexico: Socorro Co., 1 ♀, Magdalena [UK]; Texas: Presidio Co., 4 ♀♀, Marfa, June-July [USNM, HEE]; Kansas: Clark Co., 3 ♀♀, 2 ♂♂, May-June [USNM, UK]; Iowa: Kossuth Co., 1 ♂, Buffalo Creek, 16 Aug. [USNM]; Indiana: Marion Co., 1 ♀ [MCZ]; Georgia: Rabun Co., 1 ♀, Clayton, 2000 feet, 18 May [CU]; North Carolina: Chatham Co., 1 ♀, Siler City, 9 Aug. [HEE].

3a. **Pompilus (Arachnospila) fumipennis fumipennis** Zetterstedt

Pompilus fumipennis Zetterstedt, 1838, Insecta Lapponica I, p. 438. [Type: ♀; Lapland (no further data); (location, if still extant, not known to present writer).]

Arachnospila septentrionalis Kincaid, 1900, Proc. Wash. Acad. Sci., 2: 509. [Lectotype: ♀ Kukak Bay, Alaska, 4 July 1899, on flowers of *Heracleum lanatum* (T. Kincaid); U.S.N.M. no. 5313.]

Arachnophila septentrionalis Ashmead, 1902, Proc. Wash. Acad. Sci., 4: 134. —Banks, 1945, Psyche, 52: 105.

Pompilus borealis Aurivillius, 1907, Ent. Tidskr., 28: 14, 19. [Described from ♀ and ♂ from northern Sweden; whereabouts of types not known to present author.]

Psammochares lasiope Banks, 1919, Canad. Ent., 51: 81. [Type: ♀; Saranac Lake, N. Y., 26 Aug. 1916; C.U. no. 676.]—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 986.—Procter, 1938, Biol. Survey Mt. Desert Reg., VI, Insecta, p. 430. [Bar Harbor, Me.]

Psammochares (*Psammochares*) *fumipennis* Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, p. 195.

Ammosphex fumipennis Wilcke, 1943, Overdr. uit Med. van de Landbouwhoogeschool Wageningen, 47: 53.

Pompilus septentrionalis Strickland, 1947, Canad. Ent., 79: 124. [Alta.]

Pompilus lasiops [*sic*] Strickland, 1947, Canad. Ent., 79: 124.

Pycnopompilus lasiope Dreisbach, 1950, Amer. Midl. Nat., 43: 593, 596, 598, fig. 48.

Pompilus (*Arachnospila*) *fumipennis fumipennis* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

This Holarctic species is the most boreal of our Pompilidae. The synonymy of *septentrionalis* Kincaid and *lasiope* Banks with *fumipennis* Zetterstedt was established after a study of Wilcke's (1943) careful description and figures, and after study of a pair of specimens from Finland sent to me by Dr. P. M. F. Verhoeff and determined by him as *fumipennis*. These compare very closely with American specimens, even to the male terminalia.

This species, unlike the preceding two, is rather constant in its size and morphological features. The tarsal comb, the antennal formula, and the pilosity never vary greatly from the mean. The ocelli form an acute angle in front, and in the female the postocellar and ocello-ocular lines are about equal. The shape of the subgenital plate (Fig. 220) readily distinguishes the male. Typical *fumipennis* is easily recognized by its color, for it is the only member of the subgenus in our fauna which is partly red.

FEMALE.—Length 10.5 (8.5-13) mm. Color black, the upper outer and sometimes the middle inner orbits with a very small pale streak, the basal two segments of the abdomen for the greater part bright rufo-ferruginous, sometimes also part of the third segment. Pubescence brownish, usually somewhat silvery on the posterior part of the middle and hind coxae. Wings lightly infuscated, darker along the outer margin, iridescent or slight violaceous. Scape somewhat hairy below; clypeus, front, vertex, temples, and prothorax with abundant erect hair; remainder of thorax, including the coxae and to some extent the femora, barely to moderately hairy; propodeum and base of the first abdominal tergite which considerable hair; venter and apical tergite somewhat setose.

Clypeus about three times as broad as high, its apical margin very slightly arcuately concave. Front of moderate breadth, the middle interocular distance varying from .57 to .6 times the transfacial distance. Inner orbits converging noticeably above, the upper interocular distance from .72 to .82 times the lower. Ocelli forming an angle in front which is nearly always less than a right angle, the postocellar and ocello-ocular lines about equal. First four antennal segments in a ratio of about 15 : 5 : 23 : 20, segment 3 equal to from .8 to .95 times the upper interocular distance.

Postnotum nearly as long as the metanotum, transversely striate on the anterior half. Median line of propodeum weakly impressed. Front tarsus with a comb of slender spines which are from 1.5 to 3 times as long as the width of the tarsus; basitarsus with three comb-spines, rarely a small fourth one. Venation as in *scelestus* (Fig. 241).

MALE.—Length 9.5 (7.5-11.5) mm. Color and pubescence as in the female; sides of the lower front often silvery; wings as in the female. Scape at most very slightly hairy; clypeus, front, vertex, temples, and propleura with considerable erect hair; front coxae, thoracic dorsum, and propodeum with more sparse erect hairs; pleura, remaining coxae, and base of the first abdominal tergite usually slightly hairy.

Clypeus about 2.5 times as broad as high, its apical margin slightly concave. Front broad, the middle interocular distance usually about .63 times the transfacial distance; upper interocular distance usually slightly less than the lower interocular. Ocelli forming an acute angle in front, the postocellar line equal to or less than the ocello-ocular. First four antennal segments in a ratio of about 10 : 5 : 15 : 14, the third segment more than 3

times as long as thick. Thoracic features as in the female except for the usual sexual differences.

Sixth abdominal sternite with a deep V shaped apical emargination. Subgenital plate (Fig. 220) strongly keeled on the basal part, the keel abruptly and concavely declivous on the posterior half, with a series of small setae on the median line. Genitalia (Fig. 189) with the parameres long, somewhat expanded apically, the apex a little more rounded than in *sceleslus*, the outer margin fringed with long setae. Digiti somewhat variable in shape, but never as broadly spatulate as in *sceleslus*, and with a number of rather long setae at the apex. Parapenials somewhat broadened toward the apex, about as long as the aedoeagus, the latter simple, subtruncate apically.

Distribution.—This form is circumpolar in distribution; in North America it ranges transcontinentally in the Hudsonian and Canadian Zones, except from British Columbia and Alberta southward in the Rockies and Coastal Ranges, where it is replaced by subspecies *eureka* Banks.

Specimens seen: 43 (27 ♀♀, 16 ♂♂). Labrador: 1 ♀, Matamek River, 11 Aug. [MCZ]; New Brunswick: 2 ♀♀, 1 ♂, Nerepis, Aug. [USNM]; Quebec: 1 ♀, Laniel, 10 June [CNC]; 1 ♂, Seven Islands, 25 Aug. [CNC]; Ontario: 1 ♀, Westree, 28 July [CNC]; New York: Essex Co., 1 ♀, Heart Lake, 15 Aug. [CU]; 1 ♀, Wilmington, 20 Aug. [MCZ]; Franklin Co., 1 ♀, Saranac Lake, 26 Aug. [CU]; Minnesota: Clearwater Co., 1 ♂, Itasca Park, 17 June [Minn.]; Itasca Co., 1 ♂, Grand Rapids, 7 July [Minn.]; Lake Co., 1 ♀, Finland, 20 Aug. [Minn.]; Cook Co., 1 ♀, Poplar Lake, 10 Aug. [CU]; North Dakota: Bottineau Co., 1 ♂, Turtle Mts. [USNM]; Saskatchewan: 1 ♀, Harlan, 10 Aug. [CNC]; 1 ♀, Pike Lake, 30 May [CNC]; 1 ♂, Great Deer, 26 May [CNC]; Alberta: 2 ♀♀, 1 ♂, Banff, June-Aug. [USNM, CNC]; 1 ♀, Bilby, 28 July [MCZ]; 2 ♀♀, 2 ♂♂, Edmonton, June-Aug. [MCZ]; 1 ♀, Nordegg, 26 July [Alta.]; 1 ♀, Peace River, 4 Aug. [CNC]; 2 ♀♀, 1 ♂, Wabamun, June-July [Alta.]; British Columbia: 1 ♀, Glacier [ANSP]; 1 ♂, Lower Post, 17 June [CNC]; 4 ♂♂, Fort Nelson, June [CNC]; Washington: Mt. Rainier Nat. Park, 1 ♀, Paradise Valley, July [CAS]; Northwest Territories: 1 ♀ [CNC]; 1 ♀, Yellowknife, 10 Aug. [CNC]; Yukon: 1 ♂, Whitehorse, 1 July [CNC]; Alaska: 2 ♀♀ Kukak Bay, 4 July [USNM].

3b. **Pompilus (Arachnospila) fumipennis eureka** (Banks)

Psammochares eureka Banks, 1919, Bull. Mus. Comp. Zool., 63: 231-232. [Type: ♀; Ingleside, Calif., 25 Aug. 1908 (J. C. Bradley); M.C.Z. no. 10,397.[11]]

[11] Banks' male paratypes [M.C.Z. and C.U.] do not belong to this species, but to two species of *Anoplius s. str.*

Psammochares catalinae Banks, 1933, Psyche, 40: 7. [Type: ♀; Mt. Lemmon, Santa Catalina Mts., Ariz., 7800 feet, 29 July 1917 (J. Bequaert); M.C.Z. no. 17,039.]

Pycnopompilus catalinae Dreisbach, 1950, Amer. Midl. Nat., 43: 587, 593, 595, 599, figs. 35, 42 and 49.

Pompilus (Arachnospila) fumipennis eureka Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

This wholly black subspecies of *fumipennis* closely resembles *arctus* and *scelestus* in outward appearance. The male is readily distinguished by the very different subgenital plate, the female by having the ocelli forming an acute angle in front, the lateral ocelli about as close to the eyes as to one another.

FEMALE.—Length 10.5 (7.5-13) mm. Color black, the upper outer and often the middle inner orbits with a very small pale streak. Pubescence very dark, over most of the body reflecting deep bluish or violet, usually not strongly. Front wings moderately infuscated, darker along the margin, violaceous; hind wings lightly infuscated, darker apically. Scape hairy beneath; clypeus, front, vertex, temples, and propleura rather densely hairy; entire thorax, front coxae, and propodeum with abundant hairs; middle and hind coxae and to some extent the femora, slightly hairy; base of the first abdominal tergite, the apical tergite, and the venter somewhat setose. Structural features as described under the nominate subspecies.

MALE.—Length 8.5 (6-11) mm. Color black, the upper outer and middle inner orbits each with a very small pale spot; pubescence very dark, reflecting deep bluish or violet in certain lights, on the sides of the lower front often silvery. Wings somewhat more lightly infuscated than in the female. Scape slightly or barely hairy; clypeus, front, vertex, temples, and propleura with abundant erect hair; thoracic dorsum and pleura, coxate, and propodeum with considerable erect hair. Structural characters as in typical *fumipennis*.

Biology.—This form is chiefly characteristic of open places in forests at moderate or high elevations. The prey consists, so far as known, of Lycosidae. A female taken by the author at Cloudcroft, N. M., 25 July 1948, was excavating a burrow in the side of a mound of earth thrown up by a small mammal; the site was an alpine meadow surrounded by forest at an altitude of 9000 feet. The prey, which had been deposited on the earth nearby, proved to be an immature *Lycosa* sp. A female from Jackson Hole, Wyoming [USNM] is pinned with a ♂ *Trochosa pratensis* Emerton [determinations by B. J. Kaston].

Distribution.—This subspecies is distributed throughout the Canadian and Transition Zones from British Columbia and Montana south at high altitudes to New Mexico, Arizona, and southern California.

Specimens seen: 150 (86 ♀♀, 64 ♂♂). The following records are from the periphery of the range: BRITISH COLUMBIA: 2 ♀♀, Victoria, July [CNC]; 1 ♂, Courtenay, 15 July [CNC]; 1 ♀, Merritt, 13 Sept. [CNC]; 1 ♂, Carbonate, Columbia R., 7-12 July [CU]; MONTANA: Glacier Nat. Park, 1 ♂, Swift Current, 23 July [MCZ]; Meagher Co., 2 ♂♂, Belt Mts., Sept. [CNC]; WYOMING: Lincoln Co., 2 ♀♀ Jackson, Sept. [USNM]; COLORADO: Boulder Co., 1 ♀, Apr. [USNM]; NEW MEXICO: San Miguel Co., 1 ♀, 1 ♂, Beulah, Aug. [ANSP]; Otero Co., 4 ♀♀, 10 ♂♂, Cloudcroft, May-July [ANSP, HEE, UK]; Torrance Co., 1 ♂ Tajique, 25 June [UK]; ARIZONA: Cochise Co., 2 ♀♀, 1 ♂, Rustlers' Park, Chiricahua Mts., 9000 feet, 7-8 Aug. [HEE]; Pima Co., 16 ♀♀, 17 ♂♂, Mt. Lemmon, Santa Catalina Mts., 8-9000 feet, July-Aug. [CU, MCZ, HEE]; Coconino Co., 1 ♀, Flagstaff, 9 June [MCZ]; NEVADA: Elko Co., 1 ♀, Summit Pequop Mts., 17 July [CU]; CALIFORNIA: Tuolumne Co., 1 ♀, Tuolumne Meadows, 17 July [CIS]; Mariposa Co., ♀, Yosemite, 4000 feet, 12 June [CIS]; San Bernardino Co., 1 ♂, Seven Oaks, 30 May [CIS]; Riverside Co., 2 ♀♀, 1 ♂, San Jacinto Mts., June [CIS]; Los Angeles Co., 2 ♀♀, Mts. near Claremont [CU, MCZ].

G. Subgenus **ANOPLOCHARES** Banks

Psammochares (*Psammochares*) *Spissus*-group Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, pp. 153, 162, and 188.

Anoplochares Banks, 1939, Canad. Ent., 71: 225, 229. [Type: *Pompiloides rectus* Banks, 1914 (=*Pompilus apicatus* Provancher, 1882); original designation.]—Pate, 1946, Trans. Amer. Ent. Soc., 72: 72.—Dreisbach, 1949, Ent. Amer., 29: 7, 10, 38, pl. III, fig. 16.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p 935.

Ammosphex Wilcke, 1942, Ent. Berichten, 11: 25.—Wilcke, 1943, Overdr. uit Med. Landbouwhoogeschool Wageningen, 47: 47-61. [In part.]

This subgenus of *Pompilus* has become specialized in the loss of the tarsal comb, comparable to the subgenus *Anoplius* of the genus *Anoplius*. There are certain further specializations in the head and in the male terminalia, as described below, but in general the group seems very closely allied to the preceding subgenus, from which it may be derived.

Subgeneric characters.—Small to medium-sized wasps, 5.5 to 18 mm. in length. Our species wholly black. Body in general not strongly hairy;

propodeum at most very slightly hairy. Mandibles of the male unidentate, those of the female with two small, closely approximate teeth on the inner margin; apical part of the mandibles unusually smooth, flat, and shining; at the edge of the shining area is a small group of setae. Labrum exserted to about half the median length of the clypeus, the apical margin of which is distinctly concave. Malar space practically absent. Head attached unusually low on the prothorax, the vertex, in lateral view, well below the dorsal plane of the thorax.

Pronotum sharply angulate behind; postnotum a third or more the length of the metanotum. Propodeum with a strongly impressed median groove. Front tarsus of female without a comb, the basitarsus with several short spines of varying lengths, the second segment with only some very minute spines besides those at the apex. Apical tarsal segments of the female with several median spines beneath, occasionally also with one or two lateral spines. Last segment of front tarsus of male as shown in Fig. 231, not differing noticeably from the preceding subgenus. Pulvillar comb moderately well developed, as in the preceding two subgenera. Hind wing with the cubitus arising at or beyond the tip of the submedian cell. Transverse median vein of fore wing meeting the media beyond the origin of the basal. Stigma of moderate size; marginal cell rather long, from 1 to 1.5 times its own length from the wing-tip. Second and third submarginal cells both 4-sided, both somewhat narrowed above (Fig. 242).

Male subgenital plate rather narrow apically, strongly keeled (Fig. 222); basally, internally, the subgenital plate is strongly produced on each side (Fig. 223). Genitalia (Fig. 192) with the parameres slender, strongly setose; digiti strap-shaped, twisted, with dense short setae on the outer side; basal hooklets double; aedoeagus with the margins strongly sinuate, considerably broadened about two-thirds the distance from the base, then narrowed again preapically.

Biology.—Although one of our species of this subgenus is not uncommon, nothing is known of its habits. This is unfortunate, since the structural modifications of the subgenus indicate a somewhat different behavior from that of the preceding two subgenera. Adlerz [12] has studied *P.* (*Anoplochares*) *spissus* in Sweden, and found it attacking certain lycosid spiders in their burrows, and using the spider's burrow as a nest, closing over the top with debris.

Distribution.—Holarctic. Represented in Europe by such species as *spissus* Schiødte and *minutus* Dahlbom. In our fauna there are two closely related species.

[12] Adlerz, G., 1910, Handl. K. Svensk Vet.-Akad., 45: 5.

Key to Species

Females and Males

1. Fore wings subhyaline or lightly infuscated, with a darker marginal band; hind wings hyaline or subhyaline, at least basally; marginal cell usually more than its own length from the wing-tip; third discoidal cell approximately its own length from the outer wing margin; size 5.5 to 14 mm.
1. **apicatus** Provancher

Fore and hind wings wholly fuliginous, with or without a darker marginal band; marginal cell not or but slightly more than its own length from the wing-tip; third discoidal cell less than its own length from the outer wing margin; size generally larger, 11.5 to 18 mm.
2. **similaris** (Banks)

1. Pompilus (Anoplochares) apicatus Provancher

Pompilus apicatus Provancher, 1882, Nat. Canad., 13: 35, 38. [Type: ♀; St. Hyacinthe, Quebec; Q. P. M., yellow label no. 769.]—Provancher, 1883, Nat. Canad., 14: 35.—Cresson, 1887, Synopsis Hymen., Suppl. Vol. Trans. Amer. Ent. Soc., p. 270.—Dalla Torre, 1897, Cat. Hymen., VIII, p. 273.—Strickland, 1947, Canad. Ent., 79: 124. [Alta.]

Pompiloides rectus Banks, 1914, Jour. N. Y. Ent. Soc., 22: 303. [Type: ♂; Great Falls, Va., 19 June (N. Banks); M.C.Z. no. 13,682.]—Procter, 1938, Biol. Survey Mt. Desert Reg., VI, Insecta, p. 430. [Mt. Desert, Me.]

Pompiloides apicatus Rohwer, 1916, Canad. Ent., 48: 371.

Psammochares (*Pompiloides*) *rectus* Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 987. [N. Y.]—Brimley, 1936, Jour. Elisha Mitchell Sci. Soc., 52: 125-126. [N. C.]—Brimley, 1938, Insects No. Carolina, p. 433.

Pompiloides elsinore Banks, 1919, Bull. Mus. Comp. Zool., 63: 235-236. [Type: ♀; Carbonate, Columbia R., B. C., 2600 feet, 7-12 July 1908 (J. C. Bradley); C.U. no. 687.]

Anoplochares rectus Banks, 1939, Canad. Ent., 71: 229. [Made genotype of n. gen. *Anoplochares*.]—Procter, 1946, Biol. Survey Mt. Desert Reg., VII, Insecta, p. 491.—Dreisbach, 1949, Ent. Amer., 29: 38, pl. III, fig. 16.

Pompilus rectus Krombein, 1950, Jour. Elisha Mitchell Sci. Soc., 65: 263.

Pompilus (*Anoplochares*) *apicatus* Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

This distinctive species presents few difficulties in identification. It has most commonly gone by the name *rectus*, but Provancher's type specimen of *apicatus* is in good condition, and there can be no doubt that it is conspecific with Banks' *rectus* and *elsinore*.

FEMALE.—Length 10.7 (6.5-14) mm. Color black; posterior orbits with or without a very small pale spot. Front wings subhyaline to moderately infuscated, with a darker marginal band; hind wings subhyaline, the apex infuscated; wings iridescent or slightly violaceous. Pubescence brownish, often slightly violaceous in certain lights, sometimes silvery on the lower front, coxae, pleura, and propodeum. Scape very slightly hairy; temples and propleura with abundant fine hair; clypeus, front, vertex, pronotum, and front coxae with sparse erect hairs; remainder of thorax and the propodeum with at most a few very short, fine hairs; abdominal venter and apical tergite slightly setose.

Clypeus over three times as broad as high, its apical margin concave. Front of very variable breadth, the middle interocular distance varying from .56 to .66 times the transfacial distance. Inner orbits converging slightly above, the upper interocular distance about .9 the lower. Ocelli in approximately a right triangle; postocellar line equal to or slightly greater or less than the ocello-ocular line. Antennae remarkably variable in length, the third segment sometimes not longer than the scape, and equal to but slightly more than half the upper interocular distance; at the other extreme, antennal segment 3 may be much longer than the scape and pedicel together, and equal to as much as .9 the upper interocular distance.

Propodeum with a flattened posterior declivity. Mesosternum posteriorly with a median, V-shaped emargination, on each side of which it is slightly produced. Fore wing with the marginal cell from 1.1 to 1.5 times its own length from the apex of the wing; first and third transverse cubital veins slightly to strongly arched, the second nearly straight; third discoidal cell about its own length from the outer wing margin.

MALE.—Length 9.5 (5.5-13) mm. Color black, the posterior orbits sometimes with a very slender pale spot. Fore wings hyaline or very lightly infuscated, with a darker outer marginal band; hind wings hyaline, the apex slightly infuscated. Pubescence varying from entirely fuscous to almost entirely silvery. Scape slightly hairy or not; temples and propleura with abundant fine hair; front slightly to rather densely hairy; vertex, front coxae, and usually the pronotum somewhat hairy; remainder of body without more than a few short, inconspicuous hairs.

Clypeus 2.5 times as broad as high, its apical margin slightly concave. Middle interocular distance usually approximately .6 the transfacial distance; inner orbits subparallel or diverging slightly above. Ocelli forming a right or obtuse angle in front, the postocellar and ocello-ocular lines about equal. Antennae elongate, the first four segments in a ratio of about 3 : 1 : 3 : 3, the first three segments together about equal to the upper interocular distance. Longer spur of hind tibia about three-fourths the length of the basitarsus. Wing venation as in the female.

Abdominal sternite 6 with a deep U-shaped emargination. Apical abdominal segments shown in lateral view in Fig. 222. Subgenital plate differing from that of *similaris*, shown in Fig. 223, only in having the total

length slightly less in relation to the width. Genitalia as shown in Fig. 192 and as described under the subgeneric heading.

Biology.— Although *apicatus* is a widely distributed and not uncommon species, there are no records known to me of its having been taken with a spider. It occurs chiefly in sheltered places, being particularly partial to sunny spots in woodlands, where it may often be found in association with such species as *Anoplius virginiensis* and *Pompilus arctus*. In the Great Plains, however, it often occurs in open prairie country, a very different habitat from that in which it is common farther north. The species has been taken on the flowers of wild carrot and parsnip, poison hemlock, goldenrod, *Bifora*, and *Angelica*. In the latitude of Ithaca, New York, it is an early summer species, appearing in June and disappearing in early August; in the southern extremities of the range it makes its appearance in March or April and disappears a few weeks later. There appears to be only one generation a year throughout the range.

Distribution.—This is a very widely distributed species, occurring most abundantly in the Transition Zone, where it is transcontinental in distribution; from the Great Plains eastward it occurs also in the Canadian and Upper and Lower Austral Zones, ranging as far north as Labrador and Newfoundland and as far south as southern Alabama and Texas, at least in limited numbers.

Specimens seen: 367 (176 ♀♀, 191 ♂♂). The following records appear to be marginal: NEWFOUNDLAND: 2 ♀♀, 2 ♂♂, Little River, Southwest part, July [CNC]; LABRADOR: 1 ♂, Goose Bay, 9 July [CNC]; ONTARIO: 1 ♀, Sudbury [CNC]; MANITOBA: 1 ♀, 1, ♂, Aweme, July [CNC]; SASKATCHEWAN: 1 ♀, Prince Albert, July [CNC]; ALBERTA: 1 ♂, Edmonton, June [Alta.]; BRITISH COLUMBIA: 2 ♀♀, Carbonate, 7-12 July [CU, MCZ]; WASHINGTON: Thurston Co., 1 ♂, Olympia [USNM]; CALIFORNIA: Mariposa Co., 2 ♀♀, 3 ♂♂, Yosemite, 22 May-24 June [ANSP, CAS, CIS]; UTAH: 2 ♂♂, Navajo, 17 June [UAC]; NEW MEXICO: Santa Fe Co., 2 ♀♀, 1 ♂, 9200 feet, Aug. [MCZ]; TEXAS: Cameron Co., 1 ♂, Brownsville, 20 March [USNM]; LOUISIANA: 2 ♂♂ (no further data) [USNM]; ALABAMA: Mobile Co., 1 ♀, 1 ♂, Creola, 3 Apr. [HEE]; GEORGIA: 1 ♀, Atlanta, 22 July [EU]; NORTH CAROLINA: Dare Co., 2 ♀♀, Kill Devil Hills, 5 June [KVK].

2. **Pompilus (Anoplochares) similaris** (Banks)

Anoplius similaris Banks, 1919, Canad. Ent., 51: 82. [Type: ♀; Ithaca, N. Y., 25 July 1916; C.U. no. 678.]

Psammochares (Anoplius) similaris Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 987.

Anoplochares similaris Banks, 1939, Canad. Ent., 71: 229.

Pompilus (Anoplochares) similaris Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

This species averages considerably larger than *apicatus* and its wings are wholly brownish. Structurally there are only minor differences between the two species. *P. similaris* is much more restricted in its range than *apicatus*, and occupies a different ecological niche.

FEMALE.—Length 15.5 (12.5-18) mm. Color black, the upper posterior orbits with a very slender pale spot. Front and hind wings entirely fuliginous, usually somewhat more deeply so beyond the cells. Pubescence entirely fuscous or brownish, vaguely reflecting deep metallic colors in proper light. Clypeus, front, and vertex with moderately abundant short hair; temples and propleura with denser but finer hair; pronotum and front coxae slightly hairy; remainder of thorax, and the propodeum, with at most a small amount of very short, fine hair; venter and apical tergite somewhat setose.

Front rather narrow, the middle interocular distance varying from .54 to .57 times the transfacial distance. Inner orbits converging slightly above, the upper interocular distance about .9 the lower. Postocellar and ocello-ocular lines equal, or either slightly the greater; ocelli in about a right triangle. Antennae long and slender, the first four segments in a ratio of about 30: 10: 45: 42, the third segment equal to about .9 the upper interocular distance. Venation as in *apicatus*, but the marginal cell not or very slightly more than its own length from the tip of the wing. First transverse cubital vein usually rather strongly bent about mid-way, almost angulate; second and third submarginal cells both wider than high, both somewhat narrowed above (Fig. 242). Third discoidal cell long, distinctly less than its own length from the outer wing margin.

MALE.—Length 13.5 (11.5-16.5) mm. Color black, the upper outer and middle inner orbits each with a very slender pale spot, sometimes obsolescent. Wings entirely fuliginous, often slightly violaceous. Pubescence brownish-fuscous, obscurely violaceous, on the lower front coarser and paler, usually distinctly silvery; coxae and lower sides of the thorax also sometimes silvery. Clypeus, front, vertex, temples, and propleura with rather abundant erect hair; front coxae and pronotum somewhat hairy; remainder of thorax with at most a small amount of fine, short hair; propodeum usually with some fine erect hair on the sides; venter and apical two tergites with a few short erect hairs.

Front rather narrow, the middle interocular distance varying from .57 to .6 times the transfacial distance; inner orbits subparallel, the upper interocular distance subequal to or slightly less than the lower. Ocelli in a flat triangle, the front angle greater than a right angle; postocellar and ocelloocular lines subequal. First four antennal segments in a ratio of about 3 : 1 : 3 : 3, the first three segments together equal to about 1.2 times the upper interocular distance. Venation as in the female. Characters of the abdomen very similar to those of *apicatus*. Subgenital plate (Fig. 223) of the same form as in that species, but the apical portion slightly more elongate. Genitalia showing no noticeable differences from those of *apicatus*, which are shown in Fig. 192.

Biology.—This species appears to frequent more open localities than *apicatus*, occurring in sandy places, gravel pits, fields, and along roadsides. I have taken a few specimens on the flowers of parsnip, *Pastinaca sativa*.

Distribution.—This form occurs from New England, Ontario, and Illinois south to Georgia, being an inhabitant of the Allegha-nian fauna and upper fringes of the Carolinian.

Specimens seen: 35 (20 ♀♀, 15 ♂♂). ILLINOIS: McHenry Co., 1 ♂, Algonquin [ANSP]; INDIANA: 1 ♂ (no further data) [USNM]; OHIO: 1 ♀ (no further data) [MCZ]; Ottawa Co., 1 ♂, Put-in-bay, July [MCZ]; CANADA: 1 ♀, 1 ♂ (no further data) [USNM]; ONTARIO: 1 ♀, 2 ♂♂, Toronto, 1-12 July [CNC]; 1 ♀, Ottawa [CNC]; NEW HAMPSHIRE: Cheshire Co., 1 ♀, Silver Lake, 16 July [CU]; VERMONT: Windsor Co., 1 ♀, Woodstock, 20 Aug. [USNM]; MASSACHUSETTS: Hampshire Co., 1 ♂, Amherst, 10 Aug. [Mass.]; Middlesex Co., 1 ♀, Lexington [MCZ]; CONNECTICUT: New London Co., 1 ♂ [USNM]; NEW YORK: Essex Co., 1 ♀, Keene Valley, 16 Aug. [CU]; Tompkins Co., 9 ♀♀, 3 ♂♂, Ithaca, 28 June-3 Aug. [CU, MCZ, HEE]; NEW JERSEY: 2 ♀♀, 2 ♂♂, Cape May, 7-8 July [ANSP]; PENNSYLVANIA: Lancaster Co., 1 ♂, Pequea, 8 July [USNM]; WEST VIRGINIA: Wood Co., 1 ♂, Kanawha Station, 28 June [USNM]; GEORGIA: White Co., 1 ♀, Cleveland, 9 June [EU].

XI. Genus **APORINELLUS** Banks

Pompilus Groups 13 & 14 Kohl, 1884, Verh. zool.-bot. Ges. Wien, 34: 39, 54.

Aporinellus Banks, 1911, Proc. Ent. Soc. Wash., 13: 238. [Type: *Aporus fasciatus* Smith, 1855; desig. by Banks, 1912.]—Banks, 1912, Jour. N. Y. Ent. Soc., 19: 223, 230.—Bequaert, 1919, Psyche, 26: 115-123. [Review of Nearctic species.]—Banks, 1919, Bull. Mus. Comp. Zool., 63: 230, 240.—Banks, 1934, Proc. Amer. Acad. Arts & Sci., 69: 84, 106. [Philippine species.]—Banks, 1947, Bull. Mus. Comp. Zool., 99: 429. [South American species.]—Dreisbach, 1949, Ent. Amer., 29: 5, 34, pl. I, fig. 1.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 935.

Pompiloides Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, p. 258. [Type stated to be *Pompilus albofasciatus* Radoszkovsky, 1887; *nec Pompilioides* Radoszkovsky, 1887.]—Haupt, 1929, Mitt. Zool. Mus. Berlin, 15: 149-155. —Gussakovsky, 1935, Konowia, 14: 135-150. [European species.]—Arnold, 1936, Ann. Transvaal Mus., 18: 415-421. [African species.]

Ferreoloides Haupt, 1929, Mitt. Zool. Mus. Berlin, 15: 150, 153. [Type: *Pompilus moestus* Klug, 1834; desig. by Bradley, 1944.]—Bradley, 1944, Eos, 20: 93-100. [List of Old World spp.]

Eupompiloides Gussakovsky, 1935, Konowia, 14: 141. [Type: *Pompilus moestus* Klug, 1834; monobasic.]

Ceratopompilus Bradley, 1944, Eos, 20: 95, 97. [Type: *Pompilus sexmaculatus* Spinola, 1805; original desig.]

This genus is one of the most easily recognized in the tribe. The conical processes at the posterolateral angles of the propodeum (Fig. 258 and 261), the absence of any visible evidence of the postnotum dorsally, and the loss of the second transverse cubital vein in the fore wing of the majority of North American specimens, leaving but two submarginal cells, all assist in its recognition. The genus is very likely derived from *Pompilus s. str.*, with which it has many characters in common, including the presence of small appendages at the extreme base of the subgenital plate of the male (Fig. 262), and the absence of basal hooklets in the genitalia.

As indicated above, I consider *sexmaculatus* and its allies in the Old World congeneric, in fact consubgeneric, with the American *fasciatus* and its allies. I have seen both sexes of *sexmaculatus*, and in all respects, including the male genitalia, this species very closely resembles *fasciatus*. Three Nearctic species may have either two or three submarginal cells in the fore wing; the remaining Nearctic species always have two, and all the Old World species three. This character, the only one by which *Ceratopompilus* and *Aporinellus* might be considered distinct, scarcely seems of generic or subgeneric value under the circumstances.[13] I am also inclined to regard *Ferreoloides* Haupt as a synonym of *Aporinellus*, agreeing with Arnold (1936) that the toothed or bifid condition of the claws in this genus seems of little significance. The other character cited by Bradley (1944) for separating these

[13] Two other genera of Pompilini, *Evagetes* and *Pompilus* (subgenus *Perissopompilus*), have already been considered in the present study as containing species both with two and with three submarginal cells.

two groups, the color of the apical tergite of the male, is of no significance, since the North American species, all possessing toothed claws in the female, may have the apical tergite black or white.

The Nearctic species of *Aporinellus* have commonly been separated on the basis of differences in the pattern of silvery pubescence in the female. In the present study this character has been found to have no significance whatever in the separation of species. On the basis of morphological characters, there appear to be six species of *Aporinellus* in our fauna, all showing wide differences in pubescence within themselves. It is a curious fact that in some localities all the species appear to show similar changes in the pubescence. For example, in some parts of California several of the species have the silvery pubescence greatly reduced, while in places in the Pacific Northwest there is a similar tendency in the opposite direction, that is, toward a very extensive silvery pubescence. This variation seems to be of a rather local nature, not involving any definite geographic areas. At the present time it does not seem wise to regard these variants as subspecies, although further study is clearly suggested.

Generic characters.—Small wasps, 4 to 13 mm. in length. Color predominantly black, the males always entirely so, the females sometimes in part or almost wholly rufo-ferruginous. Silvery pubescence often extensive, giving the body a banded appearance, especially on the abdomen; some females with the pubescence mostly dark. Head and prothorax usually with a few inconspicuous erect hairs; apical abdominal segments of the female with a few dark setae; body otherwise practically devoid of hair. Mandibles bidentate in the female, unidentate in the male. Labrum protruding slightly if at all from beneath the clypeus, its apical margin truncate or slightly emarginate, bristly. Clypeus wider than the lower front, its apical margin truncate. Antennae inserted rather low on the front; scape fairly long; flagellum slender, of variable length. Malar space very short.

Pronotum sloping very gradually in profile, nearly or quite as long as the mesonotum; posterior margin arcuate or nearly straight. Postnotum completely absent dorsally, or represented by a very thin line, the metanotum and propodeum in broad contact. Propodeum smooth, fairly long, in dorsal aspect with the sides nearly parallel, but converging slightly behind; posterior lateral angles produced into distinct, more or less acute conical processes (Figs. 258 and 261). Legs spinose; middle and hind tibiae sparsely but strongly spinose above; front tibiae without spines above. Front tarsus of female with a comb of long, slender spines; ultimate tarsal segments

with or without small spines beneath. Pulvillar comb moderately well developed, in the female with about 15 setulae; comb of the male much weaker, of about 8 short setulae. Claws of the female in the Nearctic species dentate, the tooth short, acute. Claws of the male dentate or subbifid, the inner claw of the front tarsus somewhat modified, bifid or subbifid; apical segment of front tarsus of male unmodified.

Fore wings slender, frequently showing a tendency to fold longitudinally along a line of weakness just above the media. Stigma very small; marginal cell small, much more than its own length from the wing-tip. Transverse median vein meeting the media before the origin of the basal; basal vein with a more or less evident arcuation between the cubitus and the subcosta. Third submarginal cell, when present, smaller than the second, sometimes petiolate; American species usually with only two submarginal cells, because of the loss of the second transverse cubital vein. Third discoidal cell with the pocket at its lower basal corner scarcely evident. Hind wings slender, the anal lobe very small; cubitus arising near the tip of the submedian cell. (Wings shown in Figs. 243-246.)

Abdomen of female stout, subfusiform, that of the male much more slender. Male subgenital plate variously shaped, but always bearing on each side basally and internally a small appendage apparently composed of closely matted long setae (Figs. 262-265), much like those of *Pompilus s. str.* and in *Hesperopompilus*. Genitalia (Figs. 195-200) with the cardo short; parapenials stout, carinate dorsally, notched near the base of the aedoeagus; basal booklets wholly wanting; basis volsellaris with a few very minute setae; digiti somewhat spatulate and bearing a few setae, the disc of the digiti with an area of minute sculpturing; parameres strong, always exceeding the other appendages, more or less short-setose.

Biology.—The species of *Aporinellus* have habits similar to those of the genus *Pompilus*, preying upon spiders of several kinds and nesting in unicellular galleries in the earth. Observations have been made upon the European *sexmaculatus* by Ferton [14] and on the American *fasciatus* by the Peckhams.[15] All host records for American species so far are of jumping spiders (Salticidae). Ferton has found *sexmaculatus* preying upon several genera of jumping spiders, and upon two genera of crab spiders (Thomisidae). The species of this genus come frequently to honeydew, and some of the species occasionally visit flowers.

[14] Ferton, C., 1897, Act. Soc. Linn. Bordeaux, 52: 114; 1901, Ann. Soc. Ent. France, 70: 124; 1908, Ann. Soc. Ent. France, 77: 571; 1911, Ann. Soc. Ent. France, 80: 371, 377.

[15] Peckham, G. W. and E. G., 1898, Wisc. Geol. Nat. Hist. Survey Bull. no. 2, p. 55.

Distribution.—This genus is widely distributed in the warmer regions of the globe, being absent, so far as I know, only from the Australian region. Bradley (1944) has presented a list of the Old World species. Banks (1947) records but one species from South America. There appear to be six species in the Nearctic fauna.

Key to Species

Females

1. Ultimate tarsal segments with two or three minute spines beneath (Fig. 255); second submarginal cell of the fore wing small, less than twice as broad as high (Fig. 245) (*Taeniatus*-group) 2

   Ultimate tarsal segments without a trace of spines beneath; second submarginal cell (or 2d plus 3d when both are present) at least twice as broad as high (Figs. 243, 244, and 246) 6

2. Abdomen entirely black; legs varying from wholly black to wholly rufous or castaneous; widely distributed in the Lower and Upper Austral Zones, and throughout the Pacific states.

   1a. **taeniatus taeniatus** (Kohl)

   Abdomen in part or wholly rufous; legs partly or wholly rufous; forms with more limited ranges, occurring in the Transition Zone east of the Pacific states 3

3. Thorax and propodeum entirely black 4

   Thorax and propodeum in part or wholly rufous 5

4. Pubescence not at all silvery; comb-spines short, the apical basitarsal spine a little more than half as long as the second tarsal segment.

   1b. **taeniatus wheeleri** Bequaert

   Pubescence extensively silvery, the abdomen with apical silvery bands on several of the tergites; comb-spines longer, the apical basitarsal spine about as long as the second tarsal segment.

   1c. **taeniatus semirufus** Banks

5. Pronotum for the most part black; mesonotum, scutellum, and metanotum black; temples, in lateral view, only about half the width of the eye.

   1d. **taeniatus baboquivari** new subspecies

   Pronotum rufous; mesonotum, scutellum, and metanotum rufous or somewhat infuscated; temples, in lateral view, nearly as wide as the eye.

   1e. **taeniatus rufus** Banks

6. Ocelli forming a compact, nearly right triangle; vertex rather narrow, the eyes noticeably convergent above, the upper interocular distance varying from .75 to .9 the lower interocular distance (Figs. 251 and 252); second submarginal cell (or 2d plus 3d when both are present) usually between 2 and 2.5 times as broad as high (Figs. 243 and 244) (*Fasciatus*-group) 7

Ocelli forming a broad, flat triangle, the front angle much greater than a right angle; vertex rather broad, the eyes usually only slightly if at all convergent above, the upper interocular distance varying from .8 to 1.0 times the lower (Fig. 250); never with more than two submarginal cells, the second usually more than 2.5 times as broad as high (Fig. 246) (*Apicatus*-group) 8

7. Head in anterior view subcircular, only slightly broader than high, the transfacial distance less than 1.15 times the facial distance, the vertex arched slightly above the tops of the eyes (Fig. 252); front in profile moderately convex ..... 2. **fasciatus** (Smith)

Head in anterior view broadly oval, distinctly broader than high, the transfacial distance usually more than 1.15 times the fascial distance, the vertex nearly flat between the tops of the eyes (Fig. 251); front in profile strongly convex ..... 4. **completus** Banks

8. Antennae (Fig. 257) short and compact, segment 3 about 3.5 or 4 times as long as thick, and equal to from .45 to .65 times the upper interocular distance; antennal segments 8 through 11 each about twice as long as thick ..... 5. **apicatus** (Banks)

Antennae (Fig. 256) more long and slender, segment 3 about five times as long as thick, and equal to from .6 to .8 the upper interocular distance; segments 8 through 11 at least three times as long as thick. 6. **sinuatus** new species

Males

1. Ocelli in a compact, nearly right triangle; vertex of moderate breadth, the crest rounded off a short distance behind the posterior ocelli; second submarginal cell of the fore wing (or 2d plus 3d when both are present) usually less than 2.5 times as broad as high (Figs. 243, 244, and 245) ... 2

Ocelli in a very broad, flat triangle, the front angle much greater than a right angle; crest of the vertex rather sharp, the vertex very broad, the upper interocular distance at least 1.2 times lower interocular; second submarginal cell usually more than 2.5 times as broad as high (Fig. 246); never with 3 submarginal cells (*Apicatus*-group) 5

2. Second submarginal cell less than twice as broad as high (Fig. 245); ventral surface of parameres of genitalia more or less completely covered with short setae, more setose than the dorsal surface (Fig. 195) (*Taeniatus*-group) ..... 1. **taeniatus** (Kohl) [16]

Second submarginal cell (or 2d plus 3d when both are present) about or somewhat more than twice as broad as high (Figs. 243 and 244); ventral surface of parameres not wholly setose, less extensively so than the dorsal surface (*Fasciatus*-group) 3

[16] This species is divisible into five subspecies on characters present in the female sex only. Males can be placed in the proper subspecies only by association with the female or, to some extent, by range.

3. Subgenital plate narrow, tectiform, the apex more or less acute (Fig. 263); apical tergite black, dark pubescent; digiti capitate, about three times as wide near the apex as at the stem (Fig. 198) . . . . 4. **completus** Banks

Subgenital plate broad, rather flat, the apical margin broadly rounded or somewhat truncate (Figs. 264 and 265); digiti more narrowly expanded apically, about twice as wide there as at the stem 4

4. Subgenital plate flat except for a very short median basal elevation (Fig. 264); apical tergite with a white spot and with silvery pubescence; disc of the digitus set at an angle to the stem, clothed with prominent clubbed setae (Fig. 196) .....2. **fasciatus** (Smith)

Subgenital plate with a very prominent median carina extending from the base about half the length of the plate (Fig. 265); apical tergite without a white spot, with or without silvery pubescence; digiti straight, the disc not clothed with clubbed setae (Fig. 197).

3. **bridwelli** new species

5. Third antennal segment about 1.5 times as long as thick, considerably shorter than the fourth (Fig. 254); genitalia with numerous straight hairs of moderate length on the digitus, the aedoeagus unsually broad (Fig. 200) .....5. **apicatus** (Banks)

Third antennal segment about 1.8 times as long as thick, only a little shorter than the fourth (Fig. 253); genitalia with a number of long, sinuate hairs at the apex of the digitus, the aedoeagus not unusually broad (Fig. 199) .....6. **sinuatus** new species

Taeniatus Species-group

In this group the second submarginal cell of the fore wing is smaller than in the two following species-groups, being from 1.4 to 1.9 times as broad as high (Fig. 245). In the female there are several minute spines beneath the apical tarsal segments (Fig. 255); there may be two or three comb-spines on the front basitarsus; the color varies from black to partly or wholly rufoferruginous.

A considerable number of specific names are available for members of this group, based principally on differences in color and pubescence in the female. However, all males belonging to the group appear to be identical, even to genitalic characters. For this reason it seems logical to consider the group as constituting a single, widely distributed, highly variable species. The described variants in the female sex may be sorted into two kinds: those which are restricted to a definite geographic area and rather constant within it (such as *rufus, semirufus,* and *wheeleri*), and those which appear to occur at widely scattered localities and which fail

to retain their identity in an extended series (such as *banksi, bequaerti,* and *californicus*). The former appear to constitute a fringe of subspecies along the northern periphery of the range of *taeniatus,* while the names in the latter group are probably best regarded as synonyms of the highly variable *taeniatus taeniatus.*

1a. **Aporinellus taeniatus taeniatus** (Kohl)

Pompilus taeniatus Kohl, 1886, Verh. zool.-bot. Ges. Wien, 36: 315, 336. [Type: ♀; Orizaba, Mexico; K. K. Naturhistorische Hofmuseum, Vienna (not seen by present writer).]

Pompilus taeniolatus Dalla Torre, 1897, Cat. Hymen., VIII, p. 326.

Aporus ferrugineipes Viereck, 1906, Trans. Amer. Ent. Soc., 32: 203. [Type: ♀; Clark Co., Kansas, May, 1962 feet (F. H. Snow); Univ. Kansas.]

Aporinellus ferrugineipes Banks, 1911, Proc. Ent. Soc. Wash., 13: 238.—Banks, 1912, Jour. N. Y. Ent. Soc., 19: 230.—Bequaert, 1919, Psyche, 26: 117, 121, 123.—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 985.

Aporinellus californicus Rohwer, 1917, Proc. U. S. Nat. Mus., 53: 240. [Type: ♀; Alameda Co., Calif., July 1907 (W. M. Giffard); U.S.N.M. no. 19,967.]—Banks, 1919, Bull. Mus. Comp. Zool., 63: 240.—Bequaert, 1919, Psyche, 26: 121.

Aporinellus banksi Bequaert, 1919, Psyche, 26: 118, 121. [Type: ♀; Lee Co., Texas, May 1907 (Birkmann); M.C.Z. no. 10,757.] New synonymy. —Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Aporinellus taeniatus Bequaert, 1919, Psyche, 26: 123. [Suggests possible synonymy of *ferrugineipes* with this species.]—Krombein, 1950, Jour. Elisha Mitchell Sci. Soc., 65: 263. [N. C.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Aporinellus bequaerti Banks, 1933, Psyche, 40: 3. [Type: ♀; El Paso, Texas, 11 July 1917 (J. Bequaert); M.C.Z. no. 17,030.]

The female of this widely distributed form varies in color from wholly black, except for the mandibles, to a condition where the legs are entirely rufous, including the coxae, and the clypeus and base of the antennae are also suffused with rufous. The amount of silvery pubescence is also very variable in this sex. The males, which have previously been confused with *fasciatus,* are always wholly black and conspicuously patterned with silvery pubescence.

FEMALE.—Length 6 (4.5-8) mm. Color black; mandibles mostly castaneo-ferruginous, the base and apex generally darker; anterior margin of the clypeus usually suffused with castaneo-ferruginous, the antennal scape sometimes so; legs varying from wholly black to wholly rufo- or castaneo-

ferruginous. Body often extensively clothed with silvery pubescence, with conspicuous bands at the apices of the basal abdominal tergites, but not always so; in some specimens the pubescence is almost entirely brownish. Wings nearly hyaline, the outer margin of the fore wing with a broad brownish band, the tip of the hind wing somewhat infuscated.

Head slightly broader than high, the vertex nearly straight across; front, in profile, rather strongly convex. Clypeus considerably wider than the lower front, about 3 times as broad as high. Middle interocular distance varying from .56 to .64 times the transfacial distance; upper interocular distance varying from .75 to .9 times the lower interocular distance. Ocelli forming a triangle the front angle of which is a right angle or less; postocellar line: ocello-ocular line about as 3:2. First four antennal segments in a ratio of usually about 23:10:27:26, segment 3 equal to from .6 to .9 the upper interocular distance.

Propodeal processes prominent, acutely pointed. Front basitarsus with either two or three comb-spines, the apical one equal to from .5 to 1.2 times the length of the second tarsal segment. Ultimate tarsal segments with two or three minute spines beneath (Fig. 255). Fore wing with the marginal cell very small, over twice its own length from the wing-tip; second transverse cubital vein always wanting, there thus being two submarginal cells, the outer one less than twice as broad as high, receiving the first recurrent vein about one-third the distance from the base, the second about .9 the distance from the base (Fig. 245).

MALE.—Length 5.5 (4-7) mm.; color black, except the mandibles yellowish in the middle, reddish at the apex. Greater part of the head and thorax clothed with a heavy silvery or somewhat glaucous pubescence; base and apex of the first abdominal tergite, and apical bands on tergites 2 to 4, conspicuously silvery; basal abdominal sternites more or less silvery. Wings hyaline or nearly so, the outer margin of the fore wing with a broad light brownish band.

Clypeus between 2.5 and 3 times as broad as high. Front rather broad, the middle interocular distance from .65 to .7 times the transfacial distance; upper interocular distance about 1.1 times the lower, the eyes thus diverging somewhat above. Ocelli in a right or acute triangle, the postocellar line usually slightly less than the ocello-ocular line. Antennae rather short, the first four segments in a ratio of about 7:3:5:6, the third segment about twice as long as thick; outer flagellar segments, except the last, not twice as long as thick. Posterior pronotal margin with a faint median angulation. Processes of the propodeum small, acute.

Abdominal sternite 6 with a pronounced V-shaped emargination. Subgenital plate strongly elevated medially, tectiform; when flattened out (Fig. 262) it is seen to be broadly spatulate, the apex more or less rounded. Genitalia (Fig. 195) with the parameres strong, slightly arched, broadest about mid-way, the ventral surface clothed everywhere except at the extreme base with small setae, the dorsal surface setose only on the apical fourth. Digiti subspatulate, the disc only a little wider than the stem, clothed with a few

simple setae of moderate length. Parapenials stout, prominently curved apically, embracing the moderately broad aedoeagus.

Biology.—This form occurs in sandy or gravelly places such as beaches, stream-banks, or small sand pits, and occasionally visits honeydew. A female taken by the author near Jacksonville, Florida, was walking along a sandy road dragging the spider *Habronattus calcaratus* (Banks) (Salticidae) [det. B. J. Kaston].

Distribution.—This is a very widely distributed form, ranging throughout the Lower and Upper Austral Zones, and the Transition Zone in the Pacific states, occurring from Guatemala to British Columbia, Minnesota, and Connecticut.

Specimens seen: 89 (69 ♀♀, 20 ♂♂). The following records are from the periphery of the range: CONNECTICUT: Hartford Co., 5 ♀♀, 1 ♂, East Hartford, 13 June-19 Sept. [HEE]; NEW YORK: Nassau Co., 1 ♀, 1 ♂, Bayville, 6 Sept. [MCZ]; 2 ♀♀, Farmingdale, 4 July [KVK]; NEW JERSEY: Cumberland Co., 1 ♀, Manumuskin, 27 July [CU]; NORTH CAROLINA: Dare Co., 6 ♀♀, Kill Devil Hills, 23-27 May [KVK]; GEORGIA: Dougherty Co., 1 ♀, Albany, 30 March [EU]; OHIO: Franklin Co., 1 ♂, 21 July [RWS]; MINNESOTA: Ottertail Co., 1 ♀, Wall Lake, 30 Aug. [Minn.]; KANSAS: Clark Co., 1 ♀, May [UK]; NEW MEXICO: Dona Ana Co., 1 ♂, Mesilla, Apr. [USNM]; ARIZONA: Maricopa Co., 1 ♂, Tempe, 31 July [MCZ]; CALIFORNIA: Inyo Co., 3 ♀♀, Whitney Portal, 6 Aug. [CIS]; Placer Co., 2 ♀♀, Tahoe, July [CAS]; BRITISH COLUMBIA: 1 ♂, Okanagan Falls, 21 July [CNC]; 1 ♀, Penticton, 7 Aug. [CNC]; MEXICO: Nuevo Leon, 1 ♀, 10 mi. S. of Linares, 24 Dec. [CIS]; GUATEMALA: 1 ♀, El Salto, Escuintla, 28 June [MCZ]; LOUISIANA: 1 ♂ (no further data) [USNM]; FLORIDA: Dade Co., 1 ♀, Royal Palm Park, July [UK].

1b. **Aporinellus taeniatus wheeleri** Bequaert new status

Aporinellus wheeleri Bequaert, 1919, Psyche, 26: 118, 122. [Type: ♀; Stony Brook Reservation, near Boston, Mass., 12 July 1919 (J. Bequaert); A.M.N.H. (not seen by present writer).]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

This form is known from a few specimens from scattered localities in the Alleghanian region of the eastern United States, and appears to represent a more northerly race of *taeniatus*. The partly or wholly ferruginous abdomen, black thorax, wholly brownish pubescence, and short tarsal comb serve to separate the female from other members of this complex.

Female.—Length 6.8 (6.5-7) mm. Color black, except marked with ferruginous as follows: mandibles except at base and apex; anterior margin of clypeus; usually the antennal scape; all the legs beyond the trochanters, except that the spurs and the tarsi are more or less infuscated; at least the basal three segments of the abdomen, sometimes the entire abdomen except that the apical segment is slightly infuscated. Pubescence very fine, brownish or somewhat cinereous, nowhere silvery. Wings hyaline, the outer margin of the fore wing broadly, lightly infuscated. Middle interocular distance about .58 times the transfacial distance; upper interocular distance about .74 times the lower; third antennal segment equal to about .8 the upper interocular distance. Front basitarsus with two short comb-spines, and an additional spine of moderate length just below the basal comb-spine; apical basitarsal comb-spine a little more than half as long as the second tarsal segment. Second submarginal cell from 1.5 to 1.7 times as broad as high.

Male.—A single male assigned tentatively to this subspecies on the basis of locality data appears indistinguishable from *tacniatus taeniatus*.

Distribution.—Alleghanian fauna, Massachusetts to North Carolina.

Specimens seen: 5 (4 ♀♀, 1 ♂). Massachusetts: Middlesex Co., 1 ♀, Stony Brook Res., 9 June 1925 (J. Bequaert) [USNM]; Suffolk Co., 1 ♀, 11 Aug. 1914 (F. X. Williams) [CIS]; New York: Tompkins Co., 1 ♂, Ithaca, in sand-pit, 24 July 1947 (H. E. Evans) [HEE]; North Carolina: Buncombe Co., 1 ♀, Valley of Black Mts., 15 Aug. 1906 (W. Beutenmuller) [AMNH]; 1 ♀, Asheville, 28 July 1939 (H. K. Townes) [Coll. H. K. Townes].

1c. **Aporinellus taeniatus semirufus** Banks new status

Aporinellus semirufus Banks, 1929, Psyche, 36: 326. [Type: ♀; Martin, So. Dakota, 12 Sept. 1925 (H. C. Severin); M.C.Z. no. 16,234.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

This subspecies is known from but four specimens. It is much like *wheeleri* in coloration, but the abundant silvery pubescence gives it an altogether different appearance.

Female.—Length 5.6 (4.5-6.5) mm. Color black, marked with bright castaneo-ferruginous as follows: mandibles except at base and apex; usually the anterior margin of the clypeus narrowly; hind legs beyond the trochanters, except the spurs and tarsi more or less infuscated; middle femora and tibiae to some extent; entire abdomen, except the apical segment slightly infuscated. Greater part of the head and thorax, including the scape and most of the legs, conspicuously silvery-pubescent; first four abdominal segments more or less silvery, the pubescence tending to form bands along

the posterior margins of the segments. Wings hyaline, the outer fourth of the fore wings lightly infuscated. Middle interocular distance about .6 the transfacial; upper interocular distance about .83 times the lower; third antennal segment equal to only about .6 the upper interocular distance. Front basitarsus with three long and slender comb-spines, the apical one equal to or a little longer than the second tarsal segment. Second submarginal cell of the fore wing about 1.5 times as broad as high, nearly triangular because of the close approach of the transverse cubital veins above.

MALE.—Unknown.

Distribution.—This form is known only from Martin, South Dakota, and Medicine Hat, Alberta, Canada.

Specimens seen: 4 ♀♀. SOUTH DAKOTA: Bennett Co., 1 ♀, Martin, 12 Sept. 1925 (H. C. Severin) [MCZ]; ALBERTA: 3 ♀♀, Medicine Hat, 20 Aug. 1916, 17 July 1917 (F. W. L. Sladen) [CNC].

1d. **Aporinellus taeniatus baboquivari** new subspecies

This interesting new form represents a stage of erythrization between that of *semirufus* and that of *rufus;* the propodeum, metapleura, most of the mesopleura, and part of the sides of the pronotum are rufous, the remainder of the thorax (except the legs) black. It further differs from *rufus* in the narrower temples, and from *semirufus* in having only two basitarsal comb-spines.

FEMALE. (Holotype).—Length 5.7 mm.; fore wing 4 mm. Mandibles castaneous in the middle, black at the base and apex; apical margin of the clypeus castaneous; remainder of head black; propleura black; pronotum black, except the anterior lateral portion slightly suffused with castaneous; mesonotum, tegulae, scutellum, and metanotum black; propodeum rufo-castaneous, the posterior rim suffused with blackish; metapleura rufo-castaneous; mesopleura rufo-castaneous except along the sutures and at the top and bottom, where it is blackish; coxae, trochanters, femora, and tibiae rufo-castaneous, those of the front legs slightly infuscated; tarsi dusky-ferruginous; abdomen bright rufo-castaneous, the apex slightly infuscated. Greater part of the head, thorax, legs, and propodeum clothed with silvery pubescence; venter silvery, the first four abdominal tergites with apical silvery bands. Wings hyaline, the outer fourth of the fore wings lightly infuscated.

Clypeus three times as broad as high. Middle interocular distance .62 times the transfacial distance; upper interocular distance .82 times the lower interocular. First four antennal segments in a ratio of 17 : 8 : 20 : 19, the third segment equal to .7 the upper interocular distance. Head, in lateral view, with the temples less than half the width of the eye. Front basitarsus with two comb-spines, the apical one slightly longer than the second

tarsal segment. Second submarginal cell of the fore wing 1.6 times as broad as high, narrowed by .8 above.

MALE.—Unknown

Distribution.—This subspecies is known from a single specimen from the Baboquivari Mts. of Arizona.

Holotype.—ARIZONA: Pima Co., ♀, Baboquivari Mts., over sandy wash, 26 April 1947 (G. H. & J. L. Sperry) [Univ. Kansas].

1e. **Aporinellus taeniatus rufus** Banks new status

Aporinellus rufus Banks, 1912, Jour. N. Y. Ent. Soc., 19: 230. [Type: ♀; Boulder, Colo., 13 Aug. 1907, on *Helianthus pumilus* (S. A. Rohwer); U.S.N.M. no. 20,121.]—Bequaert, 1919, Psyche, 26: 117, 122.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

The preceding several subspecies exhibit a progressively increasing amount of rufous coloration; in *rufus* this is carried to its ultimate, and the insect is almost wholly rufo-ferruginous. Like the preceding three, this form appears to be very local in its distribution, and is known from only a few specimens.

FEMALE.—Length 6 (5-7) mm. Body wholly bright rufo-ferruginous, except as follows: tips of the mandibles deep ferruginous; front, vertex, temples, occiput, and antennal flagellum black; mesonotum, scutellum, and metanotum sometimes somewhat infuscated; extreme ventral portion of the mesopleura sometimes blackish; tarsi somewhat infuscated apically. Body clothed with a conspicuous pubescence which on the head and thorax varies from silvery to golden, or in part somewhat ferruginous; abdomen with apical silvery bands on the first 3 or 4 tergites. Wings hyaline, the outer margin of the fore wings broadly, lightly infuscated, the apex of the hind wing very lightly infuscated. Front very broad, the middle interocular distance varying from .62 to .65 times the transfacial distance; upper interocular distance about .8 to .9 the lower. First four antennal segments in a ratio of about 25:10:25:26, the third segment equal to from .55 to .65 times the upper interocular distance. Temples strongly developed, in lateral view nearly the width of the eye. Front basitarsus with two slender comb-spines, the apical one subequal in length to the second tarsal segment. Second submarginal cell of the fore wing about 1.5 times as broad as high.

MALE.—Several males assigned tentatively to this subspecies on the basis of locality data do not differ noticeably from *taeniatus taeniatus*.

Distribution.—This form is known from several localities in Colorado and in Minnesota.

Specimens seen: 11 (7 ♀♀, 4 ♂♂). COLORADO: 1 ♀ (W. J. Fox) (no further data) [ANSP]; 3 ♂♂ (C. F. Baker) (no further data) [USNM]; Boulder Co., 2 ♀♀, Boulder, 13 Aug. 1907 and 1 June 1908 (S. A. Rohwer) [USNM, MCZ]; 1 ♀, 1 ♂, White Rocks, near Boulder, 30 July 1922 [AMNH]; Teller Co., 1 ♀, Florissant, 19 June 1908, on sand (S. A. Rohwer) [USNM]; MINNESOTA: Norman Co., 1 ♀, 24 July 1923 (A. A. Nichol) [Minn.]; Polk Co., 1 ♀, 14 Aug. 1936 (D. G. Denning) [Minn.].

Fasciatus Species-group

In this group the second transverse cubital vein of the fore wing may be preserved, resulting in three submarginal cells, though more often there are but two; the second submarginal cell (or second plus third when both are present) is generally from 2 to 2.5 times as broad as high (Figs. 243 and 244). The ultimate tarsal segments of the female are without spines beneath. The ocelli are in a fairly compact triangle, the front angle of which is a right angle or sometimes slightly greater. The conical processes of the propodeum are rather small and pointed (Fig. 258).

The three species of this group are easily separable on characters of the male terminalia, but are otherwise extremely similar. A slight difference in head shape appears to separate the females of *fasciatus* and *completus,* although this is difficult to appreciate without experience in the group. The female of *bridwelli* cannot at present be distinguished from the other two species.

2. **Aporinellus fasciatus** (Smith)

Aporus fasciatus F. Smith, 1855, Cat. Hymen. Brit. Mus., III, p. 175. [Type: ♀; Warm Springs, So. Carolina; British Museum (not seen by present writer).]—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 137, 149. —Cresson, 1872, Trans. Amer. Ent. Soc., 4: 207. [Texas.]—Packard, 1874, Guide to the Study of Insects, p. 174.—Peckham and Peckham, 1898, Wisc. Geol. Nat. Hist. Survey Bull. no. 2, p. 55. [Biology.]—Birkman, 1899, Ent. News, 10: 244.—J. Smith, 1910, Ann. Rpt. N. J. State Mus. 1909, p. 674.

Pompilus unionis Dalla Torre, 1897, Cat. Hymen., VIII, p. 330. [New name for *fasciatus,* preoccupied in the genus *Pompilus.*]

Aporinellus fasciatus Banks, 1911, Proc. Ent. Soc. Wash., 13: 238.—Banks, 1912, Jour. N. Y. Ent. Soc., 19: 223, 230, 231. [Selected genotype.]—Banks, 1912, Ent. News, 23: 108. [At flowers of *Ceanothus* in Va.]—Bequaert, 1919, Psyche, 26: 118, 121.—Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 985. [Long Island, N. Y.]—Brimley, 1936, Jour. Elisha Mitchell Sci. Soc., 52: 120. [N. C.]—Brimley, 1938,

Insects No. Carolina, p. 432.—Krombein, 1950, Jour. Elisha Mitchell Sci. Soc., 65: 263.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Aporinellus medianus Banks, 1917, Bull. Mus. Comp. Zool., 61: 97. [Type: ♀; El Cajon, Calif., 1 May (E. P. VanDuzee); M.C.Z. no. 10,005.]—Banks, 1919, Bull. Mus. Comp. Zool., 63: 240.—Bequaert, 1919, Psyche, 26: 122.

Aporinellus intermedius Banks, 1919, Bull. Mus. Comp. Zool., 63: 240, 241. [Type: ♀; Claremont, Calif. (Baker); C.U. no. 690.][17]—Bequaert, 1919, Psyche, 26: 121.

As suggested by the long list of references, *fasciatus* is one of the more common species of the genus, particularly in the southern half of the United States. The female may be told from *completus* by the more nearly circular head (Fig. 252); the male differs from all other Nearctic *Aporinellus* in having the subgenital plate almost completely flat (Fig. 264). As in several other species of this genus, females from California localities frequently have the silvery pubescence much reduced.

Female.—Length 7.5 (4-13) mm. Color black, the mandibles yellowish-brown in the middle, the tips deep ferruginous. Pubescence varying from almost wholly dark, silvery only on the lower front, parts of the pronotum, and the outer portion of the tibiae, to almost wholly silvery, brownish only on the vertex, a band just before the posterior margin of the pronotum, anterior half of the mesonotum, disc of the scutellum, the bases of abdominal tergites 2, 3, and 4, and all of segments 5 and 6, the antennal flagellum, and the apices of the legs. Wings hyaline or lightly infuscated, the outer margin of the fore wing broadly banded with fuscous, the apex of the hind wing somewhat infuscated.

Head (Fig. 252) in anterior aspect subcircular, a little broader than high, the transfacial distance varying from 1.1 to 1.15 times the facial distance, the vertex elevated slightly in an arc above the tops of the eyes; front in profile somewhat less strongly convex than in *completus*. Clypeus from 2.5 to 3 times as broad as high. Front of variable breadth, the middle interocular distance varying from .58 to .67 times the transfacial distance, averaging about .61. Upper interocular distance varying from .75 to .93 times the lower interocular distance. First four antennal segments in a ratio of about 25 : 10 : 33 : 30, segment three equal to from .67 to .97 times the upper interocular distance, a very variable factor. Ocelli forming a right angle or slightly greater in front, the postocellar line usually slightly greater than the ocello-ocular.

[17] A female paratype of *intermedius* Banks, from Owen's River, Calif., 5 Aug. 1915 (C. H. Kennedy) [M.C.Z. no. 10,803] does not belong to this species, but to *sinuatus* new species.

Processes of the propodeum rather prominent, acute or narrowly rounded apically (Fig. 258). Tarsal comb consisting of long, slender spines; basitarsus with 3 comb-pines, the apical one subequal in length to the second tarsal segment, or slightly longer or shorter. Marginal cell of the fore wing from 1.5 to 2.5 times its own length from the wing-tip. About 20 percent of the specimens examined possess three submarginal cells, the second transverse cubital vein when present erect, straight. Second submarginal cell (or 2d plus 3d when both are present) varying from 2.0 to 2.7 times as broad as high, rarely over 2.5. (See Figs. 243 and 244.)

MALE.—Length 6 (4-8) mm. Color black, the apices of the mandibles more or less ferruginous, the apical abdominal tergite with a round white spot (frequently concealed by the overlapping of the preceding tergite). Body clothed with a conspicuous silvery pubescence on the following parts: scape; head except for a band across the vertex; thorax except for a band just before the posterior margin of the pronotum (usually), the anterior part of the mesonotum, and the disc of the scutellum; propodeum; legs except the extremities; first 3 or 4 abdominal sternites; first tergite, at least in large part; broad bands along the posterior margins of tergites 2, 3, and 4; and the apical tergite. Wings hyaline, the apical margin of the fore wing with a brownish band.

Clypeus from 2 to 2.5 times as broad as high. Front broad, the middle interocular distance from .65 to .7 times the transfacial distance. Inner orbits diverging considerably above, the upper interocular distance about 1.2 times the lower. Ocelli in approximately a right triangle, the postocellar line usually a little greater than the ocello-ocular line. First four antennal segments in a ratio of about 11 : 5 : 9 : 10, segment 3 from 1.5 to 2 times as long as thick. Longer spur of the hind tibia about as long as the basitarsus, or even a little longer. Wings as in the female; fore wing with either 2 or 3 submarginal cells.

Abdominal sternite 6 with an apical V-shaped emargination, on each side of which it is somewhat produced (Fig. 259). Subgenital plate (Fig. 264) broad, nearly flat, with at most a very short median elevation at the extreme base, the apex truncate or very broadly rounded. Genitalia (Fig. 196) with the parameres strong, somewhat pointed apically and setose on their outer margins and the apical half dorsally. Digitus narrow at the base, the disc oblong and bent at an angle to the stem, provided with numerous clubbed setae of moderate length. Parapenials stout, nearly straight, much wider than the aedoeagus, which is parallel-sided, unusually slender for this genus.

Biology.—This species is usually found in sandy places; it has also been taken on flowers of Queen Anne's lace, cotton, thistle, *Rudbeckia,* and *Eriogonum,* and is a frequent visitor at honeydew. The Peckmans (1898) found it nesting in their melon patch. The prey was found to be *Maevia vittata* (Hentz), a *Phidippus,* and an

Attus (all Salticidae). The burrow is oblique, about an inch and a half deep. Spiders stung by *fasciatus* seem to recover frequently, and the Peckhams believe the wasp depends more upon packing the spider tightly into the nest than upon paralysis. They also note the peculiar habit of this wasp of filling up partially excavated burrows which it decides to abandon.

Distribution.—This species occurs transcontinentally in the Lower and Upper Austral Zones, from south central Mexico and southern Florida to southeastern New York, Michigan, Wyoming, and California.

Specimens seen: 252 (177 ♀♀, 75 ♂♂). The following records appear to be marginal: NEW YORK: Nassau Co., 1 ♂, Bayville, 6 Sept. [MCZ]; NEW JERSEY: Camden Co., 1 ♀, Clementon, 24 May [MCZ]; MARYLAND: Montgomery Co., 1 ♀, 27 June [MSV]; VIRGINIA: Fairfax Co., 2 ♀♀, Falls Church, July [AMNH, USNM]; NORTH CAROLINIA: Dare Co., 10 ♀♀, 6 ♂♂, Kill Devil Hills, 24 May-5 June [KVK]; GEORGIA: Fulton Co., 3 ♀♀, Atlanta, July [USNM, EU]; MICHIGAN: Wayne Co., 1 ♀, Detroit, Sept. [CIS]; IOWA: Story Co., 1 ♀, Ames, 9 June [USNM]; NEBRASKA: Thomas Co., 2 ♀♀, 1 ♂, Halsey, 30 Aug.-3 Sept. [Minn.]; COLORADO: Teller Co., 1 ♀, Florissant, 12 June [MCZ]; UTAH: Duchesne Co., 1 ♀, No. fork Duchesne R., 13 July [CU]; WYOMING: Sweetwater Co., 1 ♀, Green River, 6100 feet, 2 July [AMNH]; NEVADA: Lyon Co., 2 ♀♀, Yerington, 5 July [CU]; CALIFORNIA: Tulare Co., 1 ♀, Lemon Cove, 10 July [CU]; San Joaquin Co., 1 ♀, Stockton, 20 Aug. [CAS]; Contra Costa Co., 3 ♀♀, Antioch, July, Oct. [CIS, CAS]; MEXICO: Baja California, 1 ♀, San Domingo, 23 Oct. [CAS]; Morelos, 1 ♀, Cuernavaca, Apr. [USNM]; Tamaulipas, 1 ♀, Victoria, 15 Mch. [USNM]; FLORIDA: Dade Co., 5 ♀♀, Mch., Apr., Oct. [AMNH, MCZ].

3. **Aporinellus bridwelli** new species

This species is closely allied to the preceding, but the male subgenital plate (Fig. 265) possesses a strong carina on its basal half, and the genitalia (Fig. 197) exhibit a number of differences.

FEMALE.—Unknown, or at least not separable at the present time from other members of this species-group.

MALE (Holotype).—Length 6 mm.; fore wing 4.5 mm. Color black, the apical half of the mandibles castaneous, tipped with ferruginous. Wings hyaline, the veins brownish, the outer margin of the fore wing with a brownish band. Head, thorax, propodeum, and legs clothed almost entirely with a heavy silvery pubescence; first 4 abdominal sternites silvery, the first tergite silvery except for a brownish spot in the middle, tergites 2, 3, and 4 with broad apical silvery bands; apical tergite dark.

Clypeus 2.2 times as broad as high. Front strongly convex, broad, the middle interocular distance .65 times the transfacial distance. Inner orbits diverging above, the upper interocular distance 1.15 times the lower interocular. Ocelli in about a right triangle; postocellar line: ocello-ocular line about as 9 : 8. First four antennal segments in a ratio of 9 : 4 : 8 : 9, segment three about twice as long as its greatest thickness.[18] Propodeum rather long, the posterior processes small. Longer spur of the hind tibia .9 the length of the basitarsus. Second submarginal cell of the fore wing 2.4 times as long as high; third submarginal cell wanting.

Abdominal sternite 6 with an apical V-shaped emargination, on each side of which it is slightly produced. Subgenital plate (Fig. 265) nearly flat, but the basal half with a very prominent, sharply elevated median carina; apical margin very broadly rounded. Genitalia (Fig. 197) with the parameres slightly curved, rather slender, the apex narrowly rounded. Digiti short and nearly straight, the disc only about twice as wide as the stem, with only some minute setae on the ventral surface, several larger ones on the upper, outer margin. Parapenials more slender than the fairly broad aedoeagus.

Five male paratypes vary in length from 5 to 7 mm. There is some variation in the pattern of silvery pubescence on the body; in one specimen there is a patch of pale pubescence on the apical tergite. In two specimens there are three submarginal cells, the third petiolate in one, sessile in the other. The genitalia are very similar in all specimens, but the subgenital plate exhibits considerable variation in shape and in the length of the median carina; the latter is often shorter than in the type, but it is always much more prominent than the small basal elevation of *fasciatus*. Two of the paratypes are lacking heads. In addition to the antennae, the holotype is also lacking the left front leg, the right hind wing, and parts of several tarsi.

Distribution.—The known range of this species extends from Kansas and Texas west to Oregon and California.

Holotype.—KANSAS: Clay Co., ♂, Aug. 1901 (J. C. Bridwell) [USNM].

Paratypes.—TEXAS: Victoria Co., 1 ♂, Victoria, 16 May 1913, on *Stillingia* (J. D. Mitchell) [USNM]; ARIZONA: Pima Co., 1 ♂, Arivaca, 13 July 1950 (R. H. Beamer) [UK]; CALIFORNIA: Inyo Co., 1 ♂, Lone Pine, 13 June 1937 (N. W. Frazier) [CAS]; Riverside Co., 1 ♂, Temecula, 4 July 1950 (E. G. Linsley) [CIS]; OREGON: Klamath Co., 1 ♂, Crater Lake, south rim, 7100 feet, 2 Aug. 1930 (H. A. Scullen) [OSC].

4. **Aporinellus completus** Banks

Aporinellus fasciatus Rohwer, 1916, Conn. Geol. Nat. Hist. Survey Bull. 22, p. 631 [*Nec* Smith, 1855; misidentification.]—Britton, 1920, Conn. Geol.

[18] The antennae are missing in the type, and this information is taken from the paratypes.

Nat. Hist. Survey Bull. 31, p. 335—Dreisbach, 1949, Ent. Amer., 29: 34, pl. I, fig. 1.

Aporinellus completus Banks, 1917, Bull. Mus. Comp. Zool., 61: 97. [Type: ♀; Yakima River, Lone Tree, Wash., 30 June 1882; M.C.Z. no. 10,004.] —Banks, 1919, Bull. Mus. Comp. Zool., 63: 240.—Bequaert, 1919, Psyche, 26: 118, 121.—Strickland, 1947, Canad. Ent., 79: 124. [Medicine Hat and Drumheller, Alta.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Aporinellus basalis Banks, 1933, Psyche, 40: 3. [Type: ♀; Tempe, Ariz. (J. Bequaert); M.C.Z. no. 17,031.]—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936. [Erroneously placed in synonymy with *fasciatus* Smith.]

This species was separated from *fasciatus* by Banks on the basis of the complete silvery vestiture. While this is the condition in most specimens from the Pacific Northwest, eastern specimens are much less extensively silvery, and some California specimens are almost wholly dark. Hence one must rely upon morphological characters in separating these species. The male of *completus* is readily recognized by the shape of the subgenital plate, but the female is less readily separated from *fasciatus* by a subtle difference in head shape (Fig. 251 as compared with Fig. 252).

Female.—Length 6.5 (5-8) mm. Color black, except that the mandibles are yellowish-brown in the middle, the apices deep ferruginous or black, and the apical margin of the clypeus sometimes pale. Wings hyaline, the outer margin of the fore wings broadly banded with pale fuscous, the apex of the hind wings lightly infuscated. Body usually extensively clothed with a heavy whitish, glaucous, or somewhat cinereous pubescence; this is replaced by a brownish, much more obscure pubescence at least on the scutellar disc, the apices of the legs, and the last two segments of the abdomen; frequently the vertex, a band just before the posterior margin of the pronotum, the mesonotum, and the bases of abdominal tergites 2, 3, and 4 are also brownish-pubescent; some California specimens have the silvery pubescence very much reduced, as in several other species of *Aporinellus*.

Head (Fig. 251) distinctly broader than high, the transfacial distance varying from 1.15 to 1.2 times the facial distance, the vertex rather flat between the eye-tops. Clypeus about three times as broad as high. Front of variable breadth, the middle interocular distance varying from .56 to .62 times the transfacial distance. Eyes converging slightly above, the upper interocular distance about .85 times the lower. First four antennal segments in a ratio of about 25 : 10 : 32 : 20, the third segment equal to from .7 to .88 times the upper interocular distance. Ocelli in about a right triangle, the postocellar line slightly greater than the ocello-ocular line. Temples

moderately developed, not wider than half the eye in lateral view; front strongly convex. Head about 1.5 times the width of the pronotum.

Propodeal processes short, acute or narrowly rounded. Spines of the tarsal comb long and slender, the one at the apex of the basitarsus about as long as the second tarsal segment. Fore wing with the second submarginal cell (or 2d plus 3d when both are present) from 2 to 2.5 times as broad as high. Third submarginal cell present in about 10% of the specimens, when present much smaller than the second.

MALE.—Length 5.5 (4-6.5) mm. Color black, the mandibles yellowish-brown apically, the tip ferruginous. Wings hyaline, the veins brownish, the apical margin of the fore wing with a brownish band. Body patterned with conspicuous silvery pubescence as in *fasciatus*, except that the apical tergite is without pale markings or pubescence.

Clypeus about 2.5 times as broad as high. Front rather broad, the middle interocular distance averaging about .67 times the transfacial distance. Inner orbits diverging above, the upper interocular distance about 1.2 times the lower. Ocelli in about a right triangle. First four antennal segments in a ratio of about 11 : 5 : 9 : 10, segment three about twice as long as its greatest thickness. Propodeum rather long, the posterolateral processes small, acute. Longer spur of the hind tibia about as long as the basitarsus. Wings as in the female.

Abdominal sternite 6 with a V-shaped apical emargination, the sides of the emargination not produced (Fig. 260). Subgenital plate narrow, strongly keeled, the apex more or less acute, the margins provided with stout setae (Fig. 263). Genitalia (Fig. 198) with the parameres long, slightly curved, setose on the outer margin and the apical third of the dorsal surface. Digitus capitate, the disc about 3 times the breadth of the stem, clothed with a few weak setae toward the upper, outer margin, one or two of which may be clubbed. Parapenials stout, slightly curved; aedoeagus simple, rather slender.

Biology.—This species is a frequent visitor to honeydew, and has also been taken on wild carrot and on sunflower. There are two host records associated with pinned specimens: (1) a female from San Francisco, Calif., labelled "dragging attid spider backward into nest hole" (F. X. Williams) [CAS]; (2) a female from Oakland, Calif. [CAS] pinned with a specimen of an immature salticid spider, probably of the genus *Habronattus* [det. B. J. Kaston]. It is possible that the Peckhams' observations on *fasciatus* (see under that species) in reality belong to this species.

Distribution.—This species occurs transcontinentally, chiefly in the Transition and Upper Austral Zones, with a number of records from the Lower Austral.

Specimens seen: 144 (88 ♀♀, 56 ♂♂). The following are marginal records: Connecticut: Hartford Co., 7 ♀♀, 3 ♂♂, East Hartford, 3 Aug.-11 Sept. [HEE]; New York: Tompkins Co., 1 ♂, Taughanic Falls, 26 July [CU]; Minnesota: Clearwater Co., 1 ♂, Itasca Park, 15 July [Minn.]; South Dakota: Fall River Co., 1 ♀, Hot Springs, 9 July [SDS]; Alberta: 1 ♂, Drumheller, 14 June [Alta.]; British Columbia: 1 ♀, Nanaimo, 28 June [CAS]; California: San Diego Co., 3 ♀♀, San Diego, June-July [Coll. H. A. Hill]; Arizona: Cochise Co., 2 ♀♀, Huachuca Mts., June [CAS]; New Mexico: Guadalupe Co., 1 ♂, Cuervo, 23 June [UK]; Texas: Brewster Co., 1 ♂, Chisos Mts., 5400 feet, 8-14 July [HEE]; Hidalgo Co., 1 ♂, 28 July [UK]; Kansas: Riley Co., 18 ♀♀, 9 ♂♂, May-Nov. [HEE, KSC]; Virginia: Fairfax Co., 2 ♀♀, 1 ♂, Dunn Loring, 6 Aug., 5 Sept. [KVK].

Apicatus Species-group

This group includes two more heavy-bodied species, in which in the female the head is only slightly wider than the prothorax. In these species the ocelli form a very broad, flat triangle on the broad vertex (Figs. 250 and 253). There are never more than two submarginal cells, and the second is very long, usually between 2.5 and 3 times as long as high (Fig. 246). In the female the eyes converge but little above, the upper interocular distance varying from .84 to 1.0 times the lower interocular. The propodeal processes are large, somewhat rounded (Fig. 261). The species of this group seem to visit flowers more frequently than those of the preceding two groups.

5. **Aporinellus apicatus** (Banks)

Aporus apicatus Banks, 1910, Jour. N. Y. Ent. Soc., 18: 126. [Type: ♂; Claremont, Calif. (Baker); M.C.Z. no. 13,721.]

Aporinellus apicatus Banks, 1912, Jour. N. Y. Ent. Soc., 19: 230.—Banks, 1919, Bull. Mus. Comp. Zool., 63: 240.—Bequaert, 1919, Psyche, 26: 122.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Aporinellus laticeps Banks, 1912, Jour, N. Y. Ent. Soc., 19: 230, 231. [Type: ♀; Boulder, Colo., on *Helianthus pumilus* (S. A. Rohwer); U.S.N.M. no. 20,122.]—Bequaert, 1919, Psyche, 26: 118, 122.

The broad front and vertex, broad ocellar triangle, and short, compact antennae (Figs. 254 and 257) distinguish this species. As in several other species of this genus, most specimens are liberally clothed with silvery pubescence, giving the insect a banded appearance, but females from California usually show a reduction

in the amount of pale pubescence, leaving the abdomen wholly dark-pubescent or with only small patches or bands of silvery pubescence at the apices of the basal tergites.

FEMALE.—Length 7.5 (5.5-10) mm. Color black, the mandibles with a subapical ferruginous band. Wings hyaline or lightly infuscated, the outer margin of the fore wing with a fuscous band, the apex of the hind wing somewhat infuscated. Pubescence varying from almost wholly brownish, silvery only on the front, clypeus, and parts of the pronotum and tibiae, to almost wholly silvery, brownish only on the flagellum, vertex, a band before the posterior margin of the pronotum, anterior half of the mesonotum, disc of scutellum, extremities of legs, bases of abdominal tergites 2, 3, and 4, and all of segments 5 and 6. All possible intermediates between these extremes occur, those with greatly reduced silvery vestiture coming chiefly from California.

Head in anterior aspect subcircular, the transfacial distance about 1.1 times the facial distance. Clypeus about 3 times as broad as high. Front very broad, the middle interocular distance varying from .6 to .68 times the transfacial distance. Eyes converging slightly if at all above, the upper interocular distance varying from .85 to 1.0 times the lower interocular. Ocelli in a very broad, flat triangle, the front angle much greater than a right angle; ocelli small and far apart; postocellar line: ocello-ocular line about as 5 : 4. Antennae (Fig. 257) relatively short, the first four segments in a ratio of about 15 : 5 : 16 : 13, segment 3 about 3.5 or 4 times as long as its greatest thickness, and equal to from .45 to .65 times the upper interocular distance; antennal segments 8 through 11 each about twice as long as thick.

Propodeal processes large, in profile rather broadly rounded (Fig. 261). Tarsal comb strong, the basitarsus with three slender comb-spines, the apical one subequal in length to the second tarsal segment. Legs relatively short and strongly spinose. Fore wing with the marginal cell about three times as long as high; second transverse cubital vein always wanting; second submarginal cell rarely less than 2.5 times as long as high.

MALE.—Length 7 (5-9.5) mm. Color black, the mandibles somewhat castaneous or ferruginous apically. Wings hyaline, the outer margin of the fore wing with a pale fuscous band, the apex of the hind wing somewhat infuscated. Body extensively patterned with conspicuous silvery pubescence, which is distributed as described under *fasciatus*. The apical abdominal tergite is silvery-sericeous, and also possesses a round white spot on the integument, often concealed by the overlapping of the preceding tergite.

Clypeus about 2.3 times as broad as high. Front broad, the middle interocular distance varying from .66 to .74 times the transfacial distance. Inner orbits diverging strongly above, the upper interocular distance about 1.25 times the lower interocular. Ocelli small and far apart, in a broad, flat triangle, the crest of the vertex rather sharp behind the posterior ocelli; head flat behind, the temples not at all developed. First four antennal segments in a ratio of about 5 : 2 : 3 : 4, segment three only

about 1.5 times as long as thick (Fig. 254); segments 9 through 12 each about 1.5 times as long as thick. Pronotum arcuate behind, with a faint suggestion of a median angulation; propodeal processes rounded or subacute apically. Venation as in the female.

Sixth abdominal sternite with a deep V shaped emargination. Subgenital plate strongly keeled; when flattened out the plate is somewhat rounded apically, not unlike that of *taeniatus*. Genitalia (Fig. 200) with the parameres very strong, somewhat tapering apically, the outer margin and apical fourth of the inner margin rather strongly setose. Digiti short, somewhat spatulate, with numerous setae on the disc, a few of which are clubbed. Parapenials somewhat curved, rather stout, but not as wide as the aedoeagus, which is of unusual breadth.

Biology.—This species appears to visit flowers more frequently than other members of the genus. It has been taken on *Baccharis, Chrysothamnus, Heterotheca, Helianthus, Ratibida, Sphaeralcea, Gossypium, Cleome, Eriogonum, Euphorbia,* and *Tephrosia.* Collection dates vary from April to November in the southern tier of states, suggesting that it may breed continually throughout the warmer months of the year.

Distribution.—This species occurs transcontinentally in the Lower and Upper Austral Zones, north to Oregon, southern Alberta, Illinois, and New Jersey; it appears to be much less common east of the 100th meridian.

Specimens seen: 117 (80 ♀♀, 37 ♂♂). The following records appear to be marginal: New Jersey: Camden Co., 1 ♀, 24 Aug. [USNM]; North Carolina: Wake Co., 1 ♀, 1 ♂, Raleigh, June, Aug. [Coll. N. C. Dept. Agri.]; Georgia: Dekalb Co., 1 ♀, Stone Mt., 13 June [EU]; Indiana: 1 ♀ (no further data) [USNM]; Illinois: Morgan Co., 2 ♂♂, Meredosia, 22 Aug. [OSC]; Iowa: Woodbury Co., 1 ♀, Sioux City, 22 July [USNM]; Kansas: Riley Co., 2 ♀♀, 1 ♂, Manhattan, Aug.-Sept. [KSC]; Alberta: 1 ♂, Medicine Hat, 1 Aug. [CNC]; Colorado: Boulder Co., 2 ♀♀, Aug. [MCZ, USNM]; Utah: Tooele Co., 1 ♀, 1 ♂, Skull Valley, 12 Aug. [UAC]; Idaho: Elmore Co., 1 ♂, Mountain Home, 3138 feet, 13 June [CIS]; Oregon: Deschutes Co., 1 ♀, Redmond, 6 Aug. [OSC]; California: Lassen Co., 2 ♀♀, Hallelujah Jct., 13 July [CIS]; Contra Costa Co., 6 ♀♀, Antioch, May-Sept. [CAS, CIS]; Mexico: Baja California, 1 ♀, 20 mi. No. of Mesquital, 27 Sept. [CAS]; Vera Cruz, 1 ♀, 29 Dec. 1940 [CIS]; Texas: Victoria Co., 4 ♀♀, 2 ♂♂, Victoria, Apr.-May [USNM]; Florida: Orange Co., 2 ♀♀, Orlando, May, June [JEG, Mass.].

6. **Aporinellus sinuatus** new species

The most striking feature of this species is the presence of several long, sinuate hairs at the apex of the digitus volsellaris of the male genitalia, hence the specific name. The males may further be told from *apicatus* by the relatively longer antenna, the third segment of which is only a little shorter than the fourth, and more than 1.5 times as long as thick (Fig. 253). The female is very similar to *apicatus,* but the antennae are notably longer and more slender (Fig. 256 as compared with Fig. 257).

Female (Allotype).—Length 7.2 mm.; fore wing 6 mm. Color black, the apical two-thirds of the mandibles reddish-brown, except the tip black. Wings subhyaline, the outer margin of the fore wing with a light fuscous band, the apex of the hind wing very lightly clouded. Body clothed with conspicuous silvery pubescence as follows: scape; entire head including base of mandibles, except for a streak across the vertex; pronotum except for a band just before the posterior margin; posterior third of mesonotum; side-pieces of the scutellum; metanotum; propodeum; all of the pleura, coxae, and the legs except the extremities; first abdominal tergite except for a portion of the sides; broad bands across the posterior margins of tergites 2, 3, and 4; all of the first four abdominal sternites. The pubescence is elsewhere brownish.

Head (Fig. 250) a little broader than high; clypeus 2.7 times as broad as high; front broad, the middle interocular distance .61 times the transfacial distance. Inner orbits diverging to the middle, then converging very slightly above; middle interocular distance 1.28 times the lower interocular distance; upper interocular distance .93 times the lower interocular. Vertex broad, the ocelli small and far apart, in a broad, flat triangle; postocellar line greater than the ocello-ocular line as 3:2. Antennae long and slender, the first four segments in a ratio of about 30:10:32:31, segment three nearly 5 times as long as its greatest thickness, equal to .73 times the upper interocular distance; antennal segments 9 through 11 each about 3 times as long as thick (Fig. 256).

Propodeal processes large, in lateral aspect rounded apically. Tarsal comb strong, with three comb-spines on the basitarsus, the apical one a little longer than the second tarsal segment. Ultimate tarsal segments not spined beneath. Marginal cell of the fore wing three times as long as high, 1.5 times its own length from the wing-tip. Second submarginal cell three times as broad as high, receiving the first recurrent vein about one-third the distance from the base, the second recurrent about .8 the distance from the base (Fig. 246).

Thirty-one female paratypes vary in size from 7 to 12 mm., the average being 9 mm. In several specimens from California and Lower California the pubescence is in large part dark; on the other hand, specimens from

Idaho and British Columbia have almost the entire body heavily silvery-pubescent except for the last two abdominal segments. In the paratype series, the middle interocular distance varies from .59 to .64 times the transfacial distance; the upper interocular distance varies from .80 to .98 times the lower interocular; antennal segment 3 varies from .64 to .80 times the upper interocular distance; the second submarginal cell varies from 2.4 to 3.1 times as long as high.

MALE (Holotype).—Length 6.5 mm.; fore wing 5 mm. Color black, the apex of the mandibles dull ferruginous, the seventh abdominal tergite with a round white spot. Wings hyaline, the outer margin of the fore wing and the apex of the hind wing lightly clouded. Body clothed with a heavy silvery pubescence as follows: scape; entire head except the vertex; pronotum except for a band just before the posterior margin; posterior half of mesonotum; side-pieces of scutellum; metanotum; propodeum; thoracic pleura, coxae, and legs except the extremities; first abdominal tergite at base, sides, and apex; broad bands along the posterior margins of tergites 2, 3, and 4; seventh tergite; sternites 1, 2, and 3, and a posterior band on 4. The pubescence is elsewhere brownish.

Clypeus 2.2 times as broad as high; front very broad, the middle interocular distance .69 times the transfacial distance; middle interocular distance 1.5 times the lower interocular distance; upper interocular distance 1.25 times the lower. Vertex very broad, the ocelli small and far apart, in a flat triangle; postocellar line: ocello-ocular line as 5:4; lateral ocelli nearer to the crest of the vertex, which is rather sharp, than to the anterior ocellus. First four antennal segments in a ratio of about 25 : 10 : 18 : 20, segment 3 about 1.8 times as long as thick; segments 9 through 11 each about 1.5 times as long as thick. (Dorsal view of head and antennae shown in Fig. 253.) Posterior pronotal margin arcuate, with a faint indication of a median angulation. Middle and hind tarsal claws dentate, but the tooth sloping forward somewhat; front tarsal claws bifid. Wing venation as described under the allotype; second submarginal cell in the type 2.9 times as broad as high.

Abdominal sternite 6 with a large, somewhat U-shaped emargination, on each side of which it is slightly produced. Subgenital plate strongly keeled, very similar to that of *completus*, shown in Fig. 263. Genitalia (Fig. 199) with the parameres rather broad, not acutely pointed apically, with an unpigmented area on the middle inner margin. Digitus volsellaris subspatulate, the disc with numerous setae along the inner margin which are short and clubbed, and on the outer side apically with several much longer, prominently sinuate setae. Parapenials rather stout, slightly curved apically; aedoeagus simple, of moderate breadth.

Twenty-four male paratypes show only very minor variations in pubescence and physical characters. This size varies from 4 to 8 mm., the average 6 mm.

Biology.—The type of *sinuatus* was collected by the author on the sandy banks of a small stream, the allotype on honeydew beneath an oak tree in an arroyo. Paratype males have been taken on the flowers of *Melilotus alba* and *Stillingia squiraria.*

Distribution.—This species appears to occur transcontinentally in the Lower and Upper Austral Zones, north to New Jersey, Kansas, Montana, and British Columbia. Its range is nearly identical with that of the sibling species *apicatus,* and like that species it is much less uncommon in the western half of the continent.

Holotype.—TEXAS: Jeff Davis Co., ♂, Limpia Canyon, Davis Mts., 5000 feet, 14-22 July 1948 (H. E. Evans) [ANSP]. *Allotype.*—TEXAS: Brewster Co., ♀, The Basin, Chisos Mts., 5400 feet, 8-14 July 1948 (H. E. Evans) [ANSP].

Paratypes.—NEW JERSEY: Camden Co., 1 ♂, Clementon, 30 May [ANSP]; GEORGIA: Decatur Co., 1 ♂, Bainbridge, 15-27 July [CU]; Gwinnett Co., 1 ♂, Lawrenceville, 10 May [MCZ]; FLORIDA: Pinellas Co., 1 ♂, Clearwater, 29 April [AMNH]; TEXAS: Bexar Co., 1 ♀, 9 May [JEG]; Culberson Co., 1 ♀, Van Horn, 5 June [CIS]; Hood Co., 1 ♀, Cresson, 1 June [USNM]; Uvalde Co., 1 ♀, Sabinal, April [USNM]; Victoria Co., 1 ♂, 16 May [USNM]; KANSAS: Meade Co., 1 ♂, 2500 feet, 10 July [UK]; Morton Co., 1 ♂, 3200 feet [UK]; Reno Co., 1 ♂, 12 Aug. [KSC]; Rooks Co., 1 ♀, 1775 feet, 9 Aug. [UK]; Scott Co., 1 ♂, 17 June [UK]; ARIZONA: Cochise Co., 1 ♀, Douglas, 29 April [USNM]; Pima Co., 1 ♂, Tucson, 14 June [HEE]; 1 ♀, 30 mi. E. of Quijotoa, 28-29 Aug. [CU]; 1 ♂, Santa Catalina Mts., 6 May [CU]; Maricopa Co., 1 ♂, Phoenix, 18 May [HEE]; 1 ♂, Marinette, 6 July [UK]; UTAH: Box Elder Co., 1 ♂, Promontory Point, 31 May [MCZ]; Tooele Co., 1 ♂, Delle, 11 Aug. [UAC]; 9 ♀♀, Skull Valley, 12 Aug. [UAC, HEE]; Uintah Co., 1 ♂, 13 July [CM]; Utah Co., 1 ♀, Lehi, 6 July [UAC]; WYOMING: Teton Co., 1 ♀, Grand Teton Park, July [CIS]; MONTANA: 2 ♀♀, 1 ♂ (no further data) [ANSP]; IDAHO: Gooding Co., 1 ♀, Tuttle, 29 July [USNM]; Twin Falls, 2 ♂♂, Hollister, 13 June, 8 Aug. [USNM]; BRITISH COLUMBIA: 1 ♀, Peachland, 22 July [CNC]; WASHINGTON: Franklin Co., 1 ♂, Pasco [USNM]; OREGON: Wasco Co., 1 ♂, The Dalles, 17 July [OSC]; CALIFORNIA: 1 ♂ (no further data) [USNM]; Kern Co., 1 ♀, Rosamond, 23 July [UK]; Lassen Co., 1 ♂, Hallelujah Jct., 13 July [CIS]; Riverside Co., 1 ♀, Pinon Flat, San Jacinto Mts., 15 June [CAS]; San Bernardino Co., 1 ♀, Cajon Pass, 27 June [CAS]; 1 ♂, 29 Palms, 14 April [CIS]; San Diego Co., 1 ♀, Jacumba, 17 July [UK]; Santa Clara Co., 1 ♀, San Antonio Valley, 14 Sept. [CIS]; Ventura Co., 1 ♀, Ventura, 15 April; MEXICO: Baja California, 2 ♀♀, Mouth of Rio Santelmo, 21 Sept. [CAS]; No DATA: 1 ♀ [JEG].

XII. Genus **ALLOCHARES** Banks

Allochares Banks, 1917, Bull. Mus. Comp. Zool., 61: 98. [Type: *Allochares bruesi* Banks, 1917 (= *azureus* Cresson, 1867); monobasic.]—Bradley, 1944, Trans Amer. Ent. Soc., 70: 148-150.—Evans, 1950, Trans. Amer. Ent. Soc., 75: 150.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Although this genus has certain characters in common with the preceding genus, *Aporinellus*, such as the presence of pointed processes on the propodeum and the absence of basal hooklets in the male genitalia, it was probably derived independently from an early *Pompilus* like form. It would seem to have no close relatives. However, the shape of the head and the propodeum somewhat suggest *Homonotus*, a highly evolved Old World genus, and it is possible that it is a relict of the old stock which gave rise to this genus. The absence of spines on the legs suggests that it is a non-fossorial genus, but as yet nothing definite is known of its biology.

Generic characters.—Small wasps, 7 to 14 mm. in length, the single known species wholly black with bluish or violet reflections. Body in both sexes devoid of all erect hair, except for a small amount on the temples and propleura. Head rather strongly convex in front and somewhat concave behind, more markedly so in the male. Maxillary palpi long and slender. Mandibles pubescent, but without setae, and without a setigerous groove beneath; inner margin with a single weak tooth. Clypeus convex; lower front, below the antennal orbits, flat; upper front strongly convex. Malar space well developed, about or more than half as long as the width of the mandibles at their base; temples not at all developed. Ocelli unusually small, situated in slight depressions.

Pronotum long, on the median line almost or quite as long as the mesonotum; streptaulus complete, the collar small, not elevated; slope of the pronotum behind the collar gradual and even. Postnotum short, transversely linear, widened on the median line. Propodeum with the spiracles removed by not more than their own length from the anterior margin; posterolaterally the propodeum is produced into a sharp, conical process on each side, between which is a strong concavity into which the basal abdominal tergite fits snugly when the abdomen is elevated; median line of propodeum strongly impressed. Legs of the female very smooth, with only a few minute spines at the apices of the tarsal segments laterally, and some barely perceptible spines on the middle and hind tibiae (even the apical tibial spines extremely minute). Legs of the male similar, but with the spines on the tibiae and basitarsi not so minute, the apices of the tibiae with a few unequal, somewhat radiating spines. Claws dentate, the tooth very weak; pulvillar pad of moderate size, but with only a fringe of very minute setulae, the pulvillar

comb thus virtually absent. Fore wing with the stigma small, the marginal cell rather large, less than its own length from the wing-tip. Second and third submarginal cells both four-sided. Basal and transverse median veins of the fore wing interstitial on the media, or nearly so; anal vein of hind wing meeting the media well before the origin of the cubitus; anal lobe small, less than one third the length of the submedian cell.

Abdomen of female stout, short, the first two segments large, the remaining segments usually telescoped rather strongly into these two; apical segment not compressed nor setose, the sting well developed. Abdomen of male also short, the apical segments in resting position telescoped into the first two, which are unusually long. Apical segments somewhat compressed, the subgenital plate strongly so, consisting of two flaps which are folded against one another. Genitalia (Fig. 193) of simple structure, without basal hooklets, the parameres slender, weakly setose.

Distribution.—The single known species of this genus is primarily Mexican in distribution, but enters the southern tier of states from California to Florida.

1. **Allochares azureus** (Cresson)

Pompilus (*Agenia*) *azureus* Cresson, 1867, Trans. Amer. Ent. Soc., 1: 131. [Type: ♀; Vera Cruz, Mexico; A.N.S.P. no. 472.]—Cresson, 1869, Proc. Boston Soc. Nat. Hist., 12: 372.

Pseudagenia azurea Kohl, 1884, Verh. zool.-bot. Ges. Wien, 34: 42.—Cameron, 1891, Biol. Centr.-Amer., Hymen. II, p. 167.—Dalla Torre, 1897, Cat. Hymen., VIII, p. 198.

Pompilus sinaloae Cameron, 1893, Biol. Centr.-Amer., Hymen. II, p. 192. [Type: ♀; Mazatlan, Mexico; British Mus. (not seen by present writer).]—Dalla Torre, 1897, Cat. Hymen., VIII, p. 323.—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 149. [Present synonymy indicated.]

Allochares bruesi Banks, 1917, Bull. Bus. Comp. Zool., 61: 98. [Type: ♀; Austin, Texas (C. T. Brues); M.C.Z. no. 10,006.]—Bradley, 1944, Trans. Amer Ent. Soc., 70: 149. [Present synonymy indicated.]

Allochares azureus Bradley, 1944, Trans. Amer. Ent. Soc., 70: 149.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

This unusual species presents no difficulties in identification. Unfortunately we have as yet no information as to its habits.

FEMALE.—Length 11 (9-13.5) mm. Color black, rendered by the very fine, velvety pubescence a rather conspicuous dark blue-violet; pubescence of the legs somewhat cinereous, that of the sides of the lower front usually grayish or silvery. Front wings moderately infuscated, with a darker apical band, violaceous; hind wings lightly infuscated, darker apically.

Clypeus about twice as broad as high, its apical margin rounded or subtruncate. Front narrow or of moderate breadth, the middle interocular

distance varying from .54 to .59 times the transfacial distance; inner orbits slightly convergent above, the upper interocular distance slightly less than the lower. Ocelli in a large triangle; postocellar line: ocello-ocular line about as 3 : 2. Antennae long and slender, the first four segments in a ratio of about 30 : 10 : 42 : 37, segment 3 equal to from .8 to 1.2 times the upper interocular distance.

Posterior pronotal margin arcuate, with a slight angulate notch on the median line. Scutellum prominent. Longer spur of hind tibia about half the length of the basitarsus.

Male.—Length 8.5 (7-10) mm. Color black; wings hyaline or nearly so, the outer margin of the fore wing and apex of the hind wing narrowly infuscated. Pubescence in large part deep blue-violet, over much of the head and thorax more or less silvery.

Clypeus about 1.8 times as broad as high, its apical margin convexly rounded, the disc strongly convex. Front strongly gibbous above the antennal orbits. Eyes diverging above, the upper interocular distance considerably greater than the lower. Antennae of moderate length, the first four segments in a ratio of about 20 : 10 : 15 : 17, segment 3 from 1.5 to 2 times as long as thick.

Subgenital plate strongly compressed, when flattened out seen to possess an apical V-shaped emargination. Genitalia (Fig. 193) with the parameres slender, sparsely setose; volsellae with a group of strong setae on the basis, some of which are clubbed, the digitus clothed with short setae except near the inner margin.

Biology.—This species has been taken on flowers of *Baccharis* and *Solidago* (Compositae).

Distribution.—The known range of this species extends from the Mexican states of Jalisco and Vera Cruz north to southern California, Arizona, Texas, Mississippi, Alabama, and Florida.

Specimens seen: 46 (30 ♀♀, 16 ♂♂). Florida: Alachua Co., 1 ♂, Gainesville, 7 April [USNM]; Duval Co., 1 ♂, Jacksonville [USNM]; Orange Co., 3 ♀♀, Orlando [CU, USNM]; Seminole Co., 1 ♀, 5 June [USNM]; Alabama: 2 ♂♂, (no further data) [USNM]; Mississippi: Jackson Co., 1 ♀, Ocean Springs, 6 Oct. [USNM]; Lafayette Co., 1 ♀, Oxford [MCZ]; Texas: Bexar Co., 3 ♀♀, May, July [JEG]; Brazos Co., 2 ♀♀, 2 ♂♂, Apr.-June, Oct. [JEG]; Brewster Co., 1 ♂, Chisos Mts., June [USNM]; Caldwell Co., 1 ♀, 1 ♂, Maxwell, 16 Apr. [JEG]; Cameron Co., 3 ♀♀, 2 ♂♂, Brownsville, Apr.-June [USNM]; Frio Co., 1 ♀, 28 June [HEE]; Hunt Co., 1 ♂, 8 July [RWC]; Jeff Davis Co., 1 ♀, Limpia Canyon, Davis Mts., July [HEE]; Hidalgo Co., 1 ♀, Edinburg [Minn.]; Lee Co., 1 ♂, Giddings, July [HEE]; Travis Co., 1 ♀, Austin [MCZ]; Uvalde Co., 1 ♀, Sabinal, April [USNM]; Arizona: Cochise Co., 1 ♀, Douglas [USNM]; Graham Co., 1 ♀, Thatcher, 8 Aug. [UAC];

Maricopa Co., 2 ♀♀, 1 ♂, Phoenix, May, Oct. [HEE]; Pima Co., 3 ♂♂, Tucson, Sept., Oct. [HEE]; California: Riverside Co., 1 ♀, Blythe, 2 Aug. [CIS]; Mexico: 2 ♀♀ (no further data) [ANSP]; Jalisco, 1 ♀, Volcano de Colima [CU]; Sonora, 1 ♀, Dec. [USNM]; Vera Cruz, 1 ♀ [ANSP].

XIII. Genus **PARACYPHONONYX** Gribodo

Paracyphononyx Gribodo, 1884, Ann. Mus. Civ. Stor. Nat. Genova, (2) 1: 306 [Type: *Paracyphononyx melanicrus* Gribodo, 1884 (= *ruficrus* Klug, 1834); monobasic.]—Arnold, 1936, Ann. Transvaal Mus., 18: 428-446. [African spp.]—Banks, 1941, Proc. Acad. Nat. Sci. Phila., 92: 352, 354. [Madagascar spp.]—Pate, 1946, Trans. Amer. Ent. Soc., 72: 98.—Evans, 1950, Trans. Amer. Ent. Soc., 75: 149.—Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 936.

Schistosalius Saussure, 1892, Grandidier's Hist. Nat. Madagascar, XX, Hymen. I, p. 313. [Type: *Salius ellioti* Saussure, 1892; designated by Ashmead, 1902.]

Paracyphonyx Ashmead, 1902, Canad. Ent., 34: 81. [Type: *Paracyphonyx metemmensis* Magretti, 1884; monobasic.]—Banks, 1934, Proc. Amer. Acad. Arts & Sci., 69: 84, 86. [Philippine spp.]

Allocyphonyx Ashmead, 1902, Canad. Ent., 34: 136. [Type: *Pompilus maurus* Cresson, 1867 (=*funereus* Lepeletier, 1845); monobasic.]—Banks, 1912, Jour. N. Y. Ent. Soc., 19: 222.—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 150-152.—Banks, 1947, Bull. Mus. Comp. Zool., 99: 436-445. [South American spp.]

Pompiloides Sustera, 1913, Verh. zool.-bot. Ges. Wien, 62: 180, 203. [*Pro Pompilioides* Radoszkowski, *nec* Radoszkowski; type stated to be *Pompilus ruficrus* Klug, 1834.]

Dicyrtomus Haupt, 1927, Deutsch. Ent. Zeitschr., Beiheft, p. 150, p. 256. [Type: *Pompilus ruficrus* Klug, 1834; original designation.]

The American species of this genus have generally been placed in Ashmead's *Allocyphonyx*, although no one has ever presented valid characters for separating *Allocyphonyx* from the Old World *Paracyphononyx*. In fact, there seem to be none. Bradley considers this group a "strongly diverging element" among the Pompilinae, and has erected the tribe Allocyphonychini for it. While it does appear to have evolved in its own way and to have developed some unusual features, the genus appears to me to fit well enough in the Pompilini. The long malar space, fully exposed labrum, compressed hypopygium of the female, serrate antennae of the male, unusual male subgenital plate, and a number of other characters serve to readily identify this genus.

Generic characters.—Medium sized wasps (6 to 20 mm. in length); our species wholly black, but exotic species often marked with red or yellow. Pubescence variable, but the propodeal declivity, at least in the males, with dense, upright pubescence, which may also be present on parts of the thorax. Head attached rather low on the prothorax, rather thin, the temples not well developed. Mandibles unidentate in both sexes. Labrum fully exposed, convex, semicircular, its median length at least half that of the clypeus. Clypeus convex transversely, its apical margin slightly concave. Malar space well developed, about as long as or longer than the antennal pedicel, at least a third as long as the width of the mandibles at their base. Front feebly convex; vertex not elevated above the eye-tops. Antennae of moderate length, in the female slender, in the male (Fig. 248) with the segments beyond the third produced on the lower side near the base, giving the antenna a weakly serrate profile.

Pronotum rather long, but on the median line shorter than the mesonotum; in profile, the slope of the pronotum is seen to be rather steep behind the collar, nearly flat posteriorly. Scutellum prominent, the side-pieces concave. Postnotum a narrow transverse band, slightly expanded dorsally, but narrowly constricted on the mid-dorsal line. Propodeum with the spiracles well removed from the anterior margin, posteriorly with a rather well-defined oblique declivity, the sides of which are sometimes prominent. Legs strongly spinose, but the female without a tarsal comb. Ultimate tarsal segments with or without spines beneath. Claws bifid in both sexes, the inner ray rather broad, truncate; pulvillar comb of from 6 to 12 setulae. Fore wing with the stigma small; radial vein somewhat angled at the third transverse cubital vein. Third submarginal cell always much narrowed above, often triangular, sometimes petiolate. Transverse median vein meeting the media beyond the origin of the basal. Hind wing with the anal vein approximately interstitial with the cubitus. (Wings of our species shown in Fig. 247.)

Abdomen of female stout, subfusiform, apically somewhat compressed, the apical sternite in particular strongly compressed, and this sternite with numerous weak erect setae. Abdomen of male slightly flattened above. Subgenital plate generally somewhat spatulate, provided apically with numerous spines and setae; basally, internally, are located paired, flap-like lobes which are provided with long setae (Fig. 249). Genitalia with the basal hooklets present, single; aedoeagus and parapenials simple; digiti elongate-spatulate, more or less setose. The parameres are the most distinctive feature of the genitalia; these are usually much expanded apically, and the margins are frequently beset with long setae. There appear to be excellent specific characters in the parameres, although the intraspecific variation is also great in some cases. (Genitalia of our species shown in Fig. 194.)

Biology.—So far as I know, nothing is known of the biology of members of this genus. Since there seems to be some structural convergence toward the genus *Notocyphus*, it is possible that they

attack certain spiders in their nests and leave them there with the egg attached to the spider, as do the species of *Notocyphus*. The structure of the clypeus and labrum also suggests the subgenus *Anoplocharcs* of the genus *Pompilus,* which has somewhat similar habits. Since our species is not uncommon throughout most of its range, it is to be hoped that someone will eventually have an opportunity to study its habits.

Distribution.—This genus is widely distributed in the warmer parts of the globe; I have seen specimens from all zoogeographic regions. Banks (1947) has treated the Neotropical species, and Arnold (1936) the Ethiopian. Only one species occurs in our fauna.

1. **Paracyphononyx funereus** (Lepeletier)

Anoplius funereus Lepeletier, 1845, Hist. Nat. des Insectes, Hymen., III, p. 449. [Type: ♂; Philadelphia, Pa.; location not known to present writer.]—J. Smith, 1910, Ann. Rpt. N. J. State Mus. 1909, p. 674.

Pompilus funereus F. Smith, 1855, Cat. Hymen. Brit. Mus., III, p. 159.—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 93. [Not identified.]—Dalla Torre, 1897, Cat. Hymen., VIII, p. 290.

Pompilus maurus Cresson, 1867, Trans. Amer. Ent. Soc., 1: 88. [Type: ♀; West Virginia (no further data); A.N.S.P. no. 414.]—[not] Provancher, 1882, Nat. Canad., 13: 35, 38.—[not] Provancher, 1883, Nat. Canad., 14: 35. [Earlier record from Canada retracted.]—Dalla Torre, 1897, Cat. Hymen., VIII, p. 300.

Allocyphonyx maurus Ashmead, 1902, Canad. Ent., 34: 136. [Made genotype of n. gen. *Allocyphonyx.*]—Banks, 1917, Bull. Mus. Comp. Zool., 61: 108.—[?] Leonard, 1926, Cornell Agri. Exp. Sta. Memoir 101, p. 985. [Saranac, N. Y.]—Brimley, 1936, Jour. Elisha Mitchell Sci. Soc., 52: 122. [N. C.]—Brimley, 1938, Insects N. Carolina, p. 433.—Bradley, 1944, Trans. Amer. Ent. Soc., 70: 152.—Dreisbach, 1946, Papers Mich. Acad. Sci., Arts, & Letters, 22: 250. [Michigan.]

Psammochares (*Allocyphonyx*) *harpalyce* Banks, 1910, Psyche, 17: 250. [Type: ♀; Southern Pines, N. C., 26 July 1909 (A. H. Manee); M.C.Z. no. 13,710.]

Paracyphononyx funereus Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 937.

This is a highly variable species. While I have not seen the type, I have little doubt that it is a highly silvery-sericeous specimen of what has usually been called *maurus* Cresson; I have seen such specimens from the vicinity of the type locality.

FEMALE.—Length 15.5 (11-20) mm. Color black; wings wholly fuliginous, violaceous. Pubescence brownish violaceous, on the occiput and often on the temples and lower front grayish or somewhat silvery. Front, temples, propleura, thoracic dorsum and pleura, coxae, and propodeum with a small amount of short erect hair; abdominal sternites and the apical tergite slightly setose, the hypopygium with numerous erect hairs.

Clypeus about twice as broad as high, its apical margin truncate or very slightly concave. Malar space of moderate length, half or more as long as the width of the mandibles at their base. Front narrow or of moderate breadth, the middle interocular distance varying from .54 to .58 times the transfacial distance. Inner orbits subparallel, the upper and lower interocular distances nearly equal. Antennae with the first four segments in a ratio of usually about 3 : 1 : 5 : 4, segment three equal to from .7 to .9 the upper interocular distance. Postocellar line usually slightly greater than the ocello-ocular line. Front with a short, impressed line in front of the anterior ocellus.

Posterior pronotal margin subangulate. Propodeal declivity short and steep; median line of propodeum lightly if at all impressed. All the tibiae, including the front pair, with prominent long spines; ultimate tarsal segments without spines beneath. Wings as shown in Fig. 247.

MALE.—Length 14.5 (8-19) mm. Color black, the apical abdominal tergite sometimes with a white spot; wings fuliginous, violaceous. Pubescence for the greater part fusco-violaceous, rarely entirely so, usually with at least the occiput and lower front grayish or silvery-pubescent; some specimens are extensively mottled with grayish-silvery pubescence, particularly on the head, pronotum, sides of the scutellum, posterior coxae, basal bands on the basal abdominal tergites, and the apical tergite. The pubescence of the propodeal declivity and disc of the metanotum is always coarse and erect, and varies in color from black to bright silvery.

Head thin, the temples not at all developed. Clypeus about twice as broad as high; malar space a little longer than in the female. Front somewhat swollen just above the antennal bases, rather flat above; inner orbits diverging slightly above. Ocelli forming an obtuse angle in front; postocellar and ocello-ocular lines about equal. Antennae as shown in Fig. 248; first four segments in a ratio of about 3 : 1 : 3 : 3, segment three from 2.5 to 3 times as long as thick. Propodeum with a short, abrupt declivity which is clothed with coarse pubescence.

Abdominal sternite 6 with a broad, shallow emargination. Subgenital plate (Fig. 249) somewhat variable in shape, the internal flaps with long setae, the apex of the plate with dense spines and setae. Genitalia (Fig. 194) with the parameres usually rather broad, fringed rather evenly with sparse long setae, the ventral surface with dense short setae near the base, otherwise bare, the dorsal surface wholly bare. The genitalia appear to show much intraspecific variation, and should not always be expected to agree closely with the figure.

Biology.—This is a mid-summer species in the northern parts of its range, but farther south occurs throughout the warmer months of the year. It is most often taken in fields and prairies, though sometimes on sand. Both sexes come frequently to flowers, and have been taken on *Asclepias, Ceanothus, Condalia, Eupatorium, Euphorbia, Melilotus, Prosopis, Solidago, Stillingia,* and *Tamarix.* Nothing further is known of the habits of this species.

Distribution.—This species occurs throughout the Lower and Upper Austral Zones, except in the Pacific states, ranging from Mexico to Utah, South Dakota, Michigan, New York, and Massachusetts.

Specimens seen: 350 (175 ♀♀, 175 ♂♂). The following are marginal records: MASSACHUSETTS: Barnstable Co., 1 ♂, Provincetown, 24 June [MCZ]; Bristol Co., 2 ♀♀, Taunton [MCZ]; CONNECTICUT: Hartford Co., 2 ♀♀, East Hartford, 6-13 Sept. [HEE]; NEW YORK: Albany Co., 1 ♀, Albany, 30 July [Mass.]; NEW JERSEY: Burlington Co., 3 ♂♂, Riverton, Aug. [ANSP]; DISTRICT OF COLUMBIA: 1 ♀, 4 ♂♂, Washington, Aug.-Sept. [USNM, MSV]; WEST VIRGINIA: 2 ♀♀ (no further data) [ANSP]; MICHIGAN: Manistee Co., 1 ♀, 24 July 1940 [Coll. R. L. Fischer]; SOUTH DAKOTA: Campbell Co., 1 ♀, Mound City, 24 Aug. [SDS]; COLORADO: 1 ♀, 1 ♂ (no further data) [ANSP]; UTAH: Cache Co., 2 ♀♀, 1 ♂, Aug. [UAC]; ARIZONA: Cochise Co., 1 ♀, 2 mi. SW of Chiricahua, 27 Aug. [ANSP]; MEXICO: Chihuahua, 1 ♀, 2 mi. W. of Matachic, 6400 feet, 7 July [AMNH]; Coahuila, 1 ♂, Buena Vista, Sierra del Carmen, 7 July [JEG]; TEXAS: Kleburg Co., 2 ♂♂, Riviera Beach, 18 June [HEE]; LOUISIANA: 1 ♀, New Orleans [USNM]; FLORIDA: 1 ♂, Key West, March [UK] (and many other Florida records).

SPECIES INCERTAE SEDIS

There remain several species which cannot be definitely placed at the present time because of inadequate descriptions and the unavailability of the types. It is possible that some of these are not Pompilini, or that they do not actually occur in the Nearctic region. These are listed below alphabetically, and a few notes are presented under each.

1. ambiguus Dahlbom

Pompilus ambiguus Dahlbom, 1845, Hymen. Europ., I, p. 452.—Dalla Torre, 1897, Cat. Hymen., VIII, p. 272.

This is an appropriately named species, for not only is the type locality ambiguous ("America"), but the description is of such

a nature as to apply to any of several species of *Anoplius* and *Pompilus*. It is described from a female having a short tarsal comb, triangular third submarginal cell, fusco-hyaline wings with a darker marginal band, and the first two abdominal segments and the base of the third rufous.

2. **bipartitus** Lepeletier

Pompilus bipartitus Lepeletier, 1845, Hist. Nat. des Insectes, Hymen., III, p. 439—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 101.

Pompilus semipartitus Dalla Torre, 1897, Cat. Hymen., VIII, p. 321.

This species, described from a female from Philadelphia, is said to be black, with the abdomen entirely testaceo-ferruginous, the wings uniformly fuscous, violaceous, the posterior pronotal margin arcuate, the propodeum with a longitudinal sulcus, the third submarginal cell narrowed toward the radius, the second slightly larger.

3. **ephippiger** Smith

Pompilus ephippiger Smith, 1855, Cat. Hymen. Brit. Mus., III, p. 158.—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 99.—Dalla Torre, 1897, Cat. Hymen., VIII, p. 287.

Lophopompilus (?) *ephippiger* Regan, 1923, Ann. Ent. Soc. Amer., 16: 179.

This species was described from a female from North America having the anterior margin of the clypeus emarginate, the posterior margin of the pronotum arcuate, the wings dark fuscous with a darker marginal band, and the second and third abdominal segments with broad yellow fasciae which are emarginate apically. I know of no North American pompilid which fits this description.

4. **fiorentinii** Dalla Torre

Pompilus brevicornis Taschenberg, 1869, Zeitschr. ges. Naturwis., 34: 50. [*Nec* Cresson, 1867.]

Pompilus fiorentinii Dalla Torre, 1897, Cat. Hymen., VIII, p. 289.

Described from Illinois and Mexico, this species is said to be blue-black, with the propodeum emarginate and bidentate posteriorly in the female, the male very similar to *amethystinus* Fabricius but with shorter antennae and the subgenital plate keeled and truncate. If the female specimen is from Mexico and is the holotype, then it is perhaps safe to regard this a synonym of *Al-*

lochares azureus (Cresson). Taschenberg's male is apparently something else.

5. **obscurus** Dahlbom

Pompilus obscurus Dahlbom, 1845, Hymen. Europ., I, p. 449.—Dalla Torre, 1897, Cat. Hymen., VIII, p. 307.

This species was described from "America"; it is stated to have violaceous wings, the base of the abdomen ferruginous, and the third submarginal cell trapezoidal. Once again one may compliment Dahlbom for the appropriateness of the name he chose, if not for his exceedingly brief description.

Addenda

Since the publication of Parts I and II of this study,[19] I have examined a considerable amount of additional material of the genera and species covered in those parts. Many of the specimens represent new locality records, and it seems desirable to make note of several range extensions at this time. A number of new host records are also reported. Since the appearance of Part I, another paper has been published by R. R. Dreisbach,[20] and the several new synonymies created by this paper are also indicated below. In the following outline, the genera and species are considered in the same order as in the main body of Parts I and II, and given the same numbers.

III. Genus **EVAGETES** Lepeletier

The following should be added to the generic synonymy:

Streptosella Dreisbach, 1950, Amer. Midl. Nat., 43: 570-574. [Type: *Streptosella steyskali* Dreisbach, 1950 (= *crassicornis crassicornis* Shuckard, 1835); by present designation.[21]] New synonymy.

Having before him three specimens of the widely distributed Holarctic *Evagetes crassicornis* Shuckard, Dreisbach recently

[19] Part I: Trans. Amer. Ent. Soc., 75: 133-270, June, 1950.
Part II: Trans. Amer. Ent. Soc., 76: 207-361, April, 1951.

[20] Dreisbach, R. R., 1950, *New Species in the Genera Anoplius, Pycnopompilus, and Streptosella, n. gen.* (*Hymenoptera: Psammocharidae*), Amer. Midl. Nat., 43: 570-599.

[21] Dreisbach designated *Streptosella michiganensis* as type of this genus, but failed to include such a species in the genus. Presumably he meant *steyskali*, the only species he had from Michigan.

described the new genus *Streptoscelia* making each of the three specimens the type of a new species. While the male genitalia of *crassicornis* are unusually distinctive, this species is in all respects clearly an *Evagetes*. Dreisbach's three species, described on the basis of minor differences in size, in color, and in shape of certain parts of the terminalia, all fall clearly within the range of variation of *crassicornis*.

2. **Evagetes parvus** (Cresson)

Mr. W. R. M. Mason, of the Division of Entomology, Department of Agriculture, Ottawa, Canada, recently collected a series of 5 females and 6 males of this species at Norman Wells, Northwest Territories, 20-28 July 1949 [CNC]. This widely distributed form was previously known from Saskatchewan and Yukon, but this record extends the known range still farther north.

6a. **Evagetes crassicornis crassicornis** (Shuckard)

The following additions should be made to the synonymy:

Streptoscelia steyskali Dreisbach, 1950, Amer. Midl. Nat., 43: 571-572, 575, figs. 1 and 2. [Type: ♂; Deerfield Township, Lapeer Co., Mich., 4 July 1937 (G. Steyskal); Univ. Michigan (not seen by present author).] New synonymy.

Streptoscelia albertensis Dreisbach, 1950, Amer. Midl. Nat., 43: 571, 572-573, 575, figs. 3 and 4. [Type: ♂; Bilby, Alberta, 20 July 1924 (O. Bryant); M.C.Z. no. 28,390.] New synonymy.

Streptoscelia stricklandi Dreisbach, 1950, Amer. Midl. Nat., 43: 571, 574, 575, figs. 5 and 6. [Type: ♂; Tofield, Alberta,[22] 22 May 1923 (E. H. Strickland); M.C.Z. no. 28,393.] New synonymy.

The situation regarding these three names is discussed under the generic heading. It is possible that *stricklandi* is somewhat intermediate between typical *crassicornis* and the smaller, all-black subspecies *consimilis* (Banks).

[22] Dreisbach gives "Toticut" as the type locality of this species, but the town of Tofield, Alberta, is clearly indicated on the label of the type.

IV. Genus **AGENIOIDEUS** Ashmead

B. Subgenus **AGENIOIDEUS** Ashmead

1. Agenioideus (Agenioideus) humilis (Cresson)

Two host records not previously reported in this study are as follows: (1) a record by Phil Rau[23] of this wasp taken at Creve Coeur Lake, Mo., with the spider *Epeira globosa* Keys., and (2) a female from Vienna, Va. (J. C. Bridwell) [USNM] pinned with the spider *Epeira pegnia* Walck. [det. B. J. Kaston]. There are now four records of the prey of this species, and in every case it is a spider of the genus *Epeira* (Epeiridae).

C. Subgenus **GYMNOCHARES** Banks

1. Agenioideus (Gymnochares) birkmanni (Banks)

There is a male of this species in the collection of Dr. H. K. Townes, of Raleigh, N. C., taken by him at Takoma Park, Maryland, 20 June 1943. This is a considerable extension of the range of this species, which was previously known from only two places east of the Mississippi, both in Georgia.

V. Genus **SERICOPOMPILUS** Howard

1. Sericopompilus angustatus (Cresson)

The occurrence of this species in Florida is confirmed by a specimen from Dunnellon, Fla., taken by D. E. Hardy on 12 July 1939 [UK]. Presumably this species will also be found to occur in other parts of the southeastern states. There is also a specimen in the author's collection from Goshen Co., Wyoming, which represents the first record from this state.

VI. Genus **EPISYRON** Schiødte

4. Episyron oregon Evans

Two additional specimens of this species have been found in the University of Kansas collections, a female from North Powder, Ore., 13 July 1931 (J. Nottingham), and a female from Trout Creek Pass, Colo., 5 July 1949 (L. D. Beamer). The latter represents the first record from Colorado and the southernmost record from the Rocky Mts.

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[23] Rau, Phil, 1922, Trans. Acad. Sci. St. Louis, v. 24, no. 7, p. 15.

VII. Genus **POECILOPOMPILUS** Howard

The common Mexican and Central American *flavopictus* Smith is now known from a single record to occur in Cameron Co., Texas. While this scarcely qualifies it as a member of the Nearctic fauna, it seems best for the sake of completeness to include it in this study. The range of *flavopictus* overlaps that of *interruptus* Say only to a very limited extent, and it differs from that form in no important structural details. While a revisionary study of the Neotropical species of *Poecilopompilus* is much needed, I shall for the present consider *flavopictus* as a subspecies of *interruptus*.

All the females of *flavopictus* which I have seen have only three basitarsal comb-spines, while the typical number in *interruptus* is four. Except for this character, *flavopictus* will key readily to *interruptus interruptus* in the key to species of *Poecilopompilus* in Part I of this study (p. 238). The following couplet will separate both sexes of *flavopictus* from typical *interruptus:*

Body clothed entirely with a fine pale pubescence which for the most part renders the integument somewhat dull; mesonotum variously colored; propodeum and first abdominal tergite in profile each strongly arched; size: female 14 (11-18) mm., male: 11.5 (8-15) mm.
2a. **interruptus interruptus** (Say)

Body clothed with a pubescence which is very fine and hardly visible for the most part, which scarcely dulls the strongly polished integument; mesonotum black, with a pair of prominent yellow stripes which are usually complete, sometimes also yellow on the sides; propodeum and first abdominal tergite in profile sloping only very slightly; size: female 12 (10-14) mm., male: 10 (8-12) mm.
2c. **interruptus flavopictus** (Smith)

2c. **Poecilopompilus interruptus flavopictus** (Smith)

Pompilus flavopictus Smith, 1862, Jour. Ent., 1: 396. [Type: ♀; Mexico (no further data); Brit. Mus. (not seen by present author).]—Smith, 1879, Descr. New Species Hymen., p. 158.—Cresson, 1867, Trans. Amer. Ent. Soc., 1: 97.—Cresson, 1869, Proc. Boston Soc. Nat. Hist., 12: 370. [Orizaba, Mex.]—Cameron, 1893, Biol. Centr.-Amer., Hymen. II, p. 210, pl. 11, figs. 27 and 27a. [Mexico (Guerrero, Tabasco, Yucatan), Guatemala, Nicaragua, Costa Rica, Panama.]—Dalle Torre, 1897, Cat. Hymen., VIII, p. 289.

Batazonus flavopictus Banks, 1925, Bull. Mus. Comp. Zool., 67: 388. [Panama.]—Banks, 1947, Bull. Mus. Comp. Zool., 99: 378. [Colombia, Surinam.]

Poecilopompilus flavopictus Bradley, 1944, Notulae Naturae, Acad. Nat. Sci. Phila., no. 145, p. 10.

Poecilopompilus interruptus flavopictus Evans, 1951, U. S. Dept. Agri., Monogr. 2, p. 927.

This distinctive form appears to be relatively constant in coloration; the head, thorax, and propodeum are conspicuously banded with yellow and black, but without ferruginous markings (except on the antennae and legs); the abdomen has alternating yellow and fusco-ferruginous bands. The integument of the head, thorax, and propodeum is strongly polished, particularly on the front and on the mesopleurum. The male terminalia appear to be identical to those of *interruptus interruptus*.

Specimens seen from the United States: 1 ♂. TEXAS: Cameron Co., 1 ♂, 3 July 1928 (L. D. Beamer) [UK]. Other specimens before me at this writing are from the Mexican states of Vera Cruz and Yucatan.

VIII. Genus **TACHYPOMPILUS** Ashmead

1a. **Tachypompilus ferrugineus ferrugineus** (Say)

During the summer of 1950, two specimens of this form were taken with their prey at Manhattan, Kansas, one inside a barn and one inside a field insectary. In both cases the prey proved to be *Lycosa helluo* Walck. In addition, a specimen from Vienna, Va. [USNM] was found to be pinned with the spider *Lycosa rabida* Walck. [determinations by B. J. Kaston].

2b. **Tachypompilus torridus unicolor** (Banks)

A specimen from Missoula, Montana, collected 11 July 1934 (H. T. Peters) [UK] represents the first record of this form from that state.

IX. Genus **ANOPLIUS** Dufour

B. Subgenus **NOTIOCHARES** Banks

1b. **Anoplius (Notiochares) amethystinus atramentarius** (Dahlbom)

This common eastern and midwestern form is now known to occur in New Mexico, two males having been taken at Las Cruces on 12 June 1950 by L. D. Beamer [UK].

D. Subgenus **ARACHNOPHROCTONUS** Howard

7c. **Anoplius (Arachnophroctonus) americanus juxtus** (Cresson)

A long series of this form has recently been collected by J. W. MacSwain of the University of California at Big Dalton Dam, Los Angeles Co., Calif. (27 ♀♀, 35 ♂♂, 25 June 1950) [CIS]. I had previously seen relatively few specimens from California. In this series the females are entirely without silvery pubescence, and the rufous coloration extends very slightly if at all to the abdominal sternites. Consequently they key out poorly to *juxtus* in my key to the species and subspecies of *Arachnophroctonus*. I confess that I am unable to present better characters for separating the subspecies of *americanus* at the present time. This is only one of many pompilids which are more or less consistently darker in the coloration of the integument and pubescence in California.

E. Subgenus **POMPILINUS** Ashmead

2. **Anoplius (Pompilinus) subcylindricus** (Banks)

A new prey record and a slight range extension may be reported for this species. A female in the U. S. National Museum, from Barcroft, Va., is pinned with a young spider of the genus *Micaria* (Clubionidae) [det. B. J. Kaston]. A male from Arivaça, Arizona, 18 July 1950 (L. D. Beamer) [UK] is the first record from this state.

7. **Anoplius (Pompilinus) californiae** Evans

A specimen of this species collected at Yermo, San Bernardino Co., Calif., 28 April 1949 [CIS] is a gynandromorph. It is essentially a female except for the left front leg, which is entirely male in character; in addition there are patches of silvery pubescence on various parts of the head and thorax not ordinarily present in the female, but suggestive of the extensive silvery pubescence sometimes present in the male.

9. **Anoplius (Pompilinus) tenebrosus** (Cresson)

A specimen of this species taken by J. G. Rozen at Whiteriver, Arizona, 19 June 1950 [UK] is the first record of this widely distributed northern species from the state of Arizona.

15. **Anoplius (Pompilinus) marginatus** (Say)

The following are new host records for this species: (1) a female taken by the author at East Hartford, Conn., 18 Aug. 1950 [HEE] with a female *Habronattus decorus* (Blackwall) (Salticidae); (2) a female from Clifton, Va. (J. C. Bridwell) [USNM] taken with the spider *Trochosa pratensis* (Emerton) [determinations by B. J. Kaston].

Summary and Conclusions: the Composition, Origin, and Phylogeny of the Nearctic Fauna of Pompilini

It is not altogether customary to conclude a taxonomic paper with a summary, for the keys, descriptions, and discussions which comprise such a treatise are commonly considered to be self-sufficient. From the stand-point of identification, they perhaps are. Yet a taxonomic study ought to have meaning to a person not actually engaged in the identification of specimens, to a person, in fact, who may not even be well acquainted with the group in question. This meaning is, however, apt to be a lost needle in a vast haystack of words unless the systematist makes some effort to assist the reader in finding it. The essence of the problem will, of course, be a consideration of the evolution of the group in question, since systematics is, within the limitations of its techniques, a study of evolution. It may be argued that in many groups of insects (including, surely, the Pompilini) our knowledge is so fragmentary as to preclude the possibility of drawing valid conclusions along these lines. Yet how few insect groups are known as well as the butterflies or the pomace-flies! This need not mean that there is no hope for the taxonomist in other groups, however, for the cautious application of principles discovered in better-known groups may be a profitable way of analyzing one's data. At any rate, on the following pages I have attempted to bring together a few facts relating to the broader aspects of the problem at hand, and to present a few tentative conclusions regarding certain aspects of the evolution of the Nearctic Pompilini.

Composition of the Nearctic fauna.—The tribe Pompilini contains 96 known species in the Nearctic fauna, or a total of 124 species and subspecies. Undoubtedly a few species remain to be

discovered, particularly in the Southwest, and undoubtedly further analysis of the fauna will enable future workers, using more refined techniques, to recognize additional subspecies. In all, about 19,000 specimens were examined in the present study, or an average of about 200 specimens per species. As would be expected, some species are abundantly present in most collections of Pompilidae, while others are known from very few specimens. Thus, while I have seen over 1000 specimens of one species, I have seen only one specimen of each of three species. The abundance of a species in collections is, of course, only very roughly indicative of its abundance in nature; however poor a criterion it may be, it is nevertheless almost the only one readily available to the taxonomist for estimating the size of a population.

It may be of interest to note parenthetically that among these 19,000 specimens were discovered five gynandromorphs. This is a rate of 1 per 3800 specimens, or .026%. While many hymenopterists have described gynandromorphs, there is little information available on the actual per cent of gynandromorphs in a long series of specimens of a tribe or genus. Krombein,[24] in a very interesting paper on gynandromorphs among the Aculeata, states that he has examined approximately 10,000 specimens of the tiphiid genus *Myzinum* and seen only one gynandromorph, which would be a percentage of .01% for this genus. I do not attach any particular significance to these figures, but they may serve to illustrate more precisely the very low incidence of gynandromorphs among these insects.

It should be pointed out that the 96 species recognized by the present author represent a very considerable reduction in the number of supposed species in our fauna. A large number of specific names have been placed in synonymy in the present study, largely as a result of three factors. First, it has been recognized that each species has a certain range of variation, which in these wasps is often surprisingly great. Since many of the Pompilini are not highly selective of their prey and use only one spider to stock the nest, it seems likely that much of this variation (in size, at least) is due to differences in food available to the larva. Secondly, a genuine effort has been made to correlate the sexes properly.

[24] Krombein, K. V., 1949, Proc. U. S. Nat. Mus., 100: 59.

As in many groups of Hymnoptera in which there is a marked sexual dimorphism, there has been a tendency in the past to apply different names to opposite sexes of the same species. In certain groups, particularly *Pompilinus*, considerable work still remains to be done in correlating the sexes. A third factor has been the recognition of the exceedingly broad ranges of many of our species. Some earlier authors have been much inclined to apply different names to virtually identical specimens from different parts of the country, on the assumption that they must be different species. It is now known that 44 species, or 46% of the total, are transcontinental in distribution.

An additional reason for the reduction in the number of species is that a number of them have been reduced to subspecific rank. In the present study 19 species, or 20% of the total, are regarded as polytypic, the remainder as monotypic. As I have already stated, I suspect that future workers will be able to discern additional subspecies, and thus increase the percentage of polytypic species. In the present study, a number of the "varieties" of earlier authors have been reduced to synonymy, since they do not appear to have any definite range. The subspecies now recognized vary all the way from color forms which, however, appear to have a definite geographic range, to forms which differ by morphological features which are sometimes fairly prominent. I have been criticized (*in litt.*) by some hymenopterists for regarding as subspecies certain allopatric forms which, while extremely similar, differ in some details of the male genitalia. If it is true that these slight differences in genitalic structure imply reproductive isolation, then these forms should, of course, be regarded as full species. However, the genitalia of these wasps are by no means lock-and-key devices, and I suspect that the reproductive isolating factors are more often behavioristic than morphological. It is apparent that workers in some other groups of Aculeata regard any form having constant genitalic differences from its relatives, however slight they may be, as being worthy of full specific rank. To my mind, it may in some cases better indicate the relationships involved to regard them as subspecies in spite of minor differences in the male genitalia, although in such cases the forms in question may well be approaching the specific level.

The 96 Nearctic species are regarded by the present author as falling into 13 genera, or a total of 25 genera and subgenera. The average is therefore 7.4 species per genus, or slightly less than 4 per subgenus. Three genera contain, in our fauna, but one species; three genera contain two species; two genera contain three species; one genus contains five species; two contain six species; one genus (*Pompilus*) contains 21 species; and one genus (*Anoplius*) contains 43 species. If the number of genera is plotted against the number of contained species, the hollow curve of Willis[25] is approached surprisingly closely for so small a group.

Again, thirteen represents a large reduction in the number of genera previously recognized in this tribe. This perhaps requires little explanation, the genus being the intangible thing that it is. It may be worth pointing out, however, that the genus is commonly conceived as a unit representing a certain level of evolutionary distinctness. It seems to me poor practice to regard the genus as merely a device for grouping species for identification's sake. Dreisbach,[26] for example, expresses this view, and defines a genus simply as "a group of species which can be separated in both sexes by means of external, easily discernible characters". This author, while defining the Pompilini (Psammocharini) more narrowly than I have done, and omitting several groups, recognizes 25 genera in the Nearctic fauna. To my mind, it is fallacious to give equal rank to such groups, for example, as *Episyron* and *Pompilinus*. The former is a discrete genus by any definition, but the latter merges into *Arachnophroctonus* on one hand, and is sometimes difficult to separate from *Anoplius* on the other. If the generic category is to have any phylogenetic significance at all, an effort must be made to apply it to stocks of approximately equal value as far as apparent degree of discreteness is concerned. Groups of lesser value may then be regarded as subgenera, and those of still less value as species-groups.

Origins of the Nearctic fauna.—If one examines the ranges of the various genera and subgenera of Pompilini, it soon becomes

[25] Willis, J. C., 1922, Age and Area, p. 195.

[26] Dreisbach, R. R., 1949, Ent. Amer., *29*: 4.

apparent that each presents a distinct facies with regard to distribution and relationships. In general, these distribution patterns may be classified as one of three types. First of all, there are those groups which are predominantly northern in distribution, ranging southward principally in the mountain systems; these for the most part have their closest relatives in Eurasia, and their distribution may be termed *Holarctic*. Secondly, there are those groups of essentially southern distribution, which range northward for the most part along the coasts and the major river systems, and which have their closest relatives in the tropics. These may be termed simply the *Tropical* element. The members of the third group, which may be called the *Sonoran* element, seem to have no close relatives either to the south or to the north; these forms are especially characteristic of the arid regions of the Southwest. It is logical to make certain deductions from these distribution patterns regarding the origins of these various elements in our fauna. This has been done in a number of other groups of insects, and the conclusions reached here do not differ radically from those reached by workers in several other groups.[27]

The largest number of Nearctic Pompilini are rather clearly *Holarctic* in their affinities. In all, nine genera or subgenera come in this category: *Evagetes, Agenioideus* (*s. str.*), *Episyron, Lophopompilus, Pompilinus, Anoplius* (*s. str.*), *Ammosphex, Arachnospila,* and *Anoplochares*. These groups include a total of 57 species, or 59% of the fauna. Several of the groups have a few representatives in the Neotropical region, but in all cases the center of distribution is decidedly northern, and each of the groups is well represented in Eurasia. This similarity between the faunas of North America and Eurasia is by no means surprising, since it is believed that a Siberia-Alaska land bridge existed through a considerable part of the Coenozoic. Presumably most or all of the Holarctic elements entered our fauna by way of Siberia and Alaska.

[27] See, for example, several papers published in the Proc. 6th Pacific Science Congress, v. 4, 1940, particularly E. C. VanDyke's *The Origin and Distribution of the Coleopterous Insect Fauna of North America* (pp. 255-268), and C. D. Michener's *The Distributional History of North American Bees* (pp. 297-303). While neither of these authors considers the Sonoran element of equal rank with the Holarctic and the Tropical, it is interesting to note that VanDyke considers the Sonoran fauna as derived chiefly from the neotropics, while Michener ranks it as a subregion of the Nearctic, and feels that it contains more elements of northern origin than of southern.

Three species of Pompilini, *Evagetes crassicornis crassicornis*, *Anoplius* (*Anoplius*) *nigerrimus*, and *Pompilus* (*Arachnospila*) *fumipennis fumipennis*, occur both in Eurasia and in northern North America. It seems possible that these forms may have entered our fauna postglacially. Another group of species may be singled out as differing from their nearest Eurasian relatives only in minor characters such as color, size, pilosity, and details of the genitalia; in this group would fall such forms, for example, as *Evagetes crassicornis consimilis*, *Anoplius* (*Anoplius*) *basalis*, *Pompilus* (*Arachnospila*) *fumipennis eureka*, and *Pompilus* (*Ammosphex*) *luctuosus*. These forms are for the most part somewhat less boreal than the first group, and may represent a somewhat earlier wave of migrants from Eurasia, perhaps during the last interglacial period. Still other species, of which *Evagetes parvus*, *Anoplius* (*Anoplius*) *virginiensis*, and *Pompilus* (*Arachnospila*) *arctus* might be cited as examples, differ in a larger number of characters from their nearest Eurasian relatives, and occur slightly farther south. A still further echelon of species includes such forms as *Evagetes hyacinthinus*, *Anoplius* (*Anoplius*) *ventralis*, *Pompilus* (*Ammosphex*) *solonus*, and others, which are predominantly Austral in distribution. A final group includes such forms as *Anoplius* (*Anoplius*) *fulgidus*, now predominantly tropical in distribution, although clearly of Holarctic origin.

It seems apparent, then, that the Holarctic members of our fauna have entered at various times within recent geological epochs, each wave of migrants over the Siberia-Alaska land bridge having been pushed southward progressively by successive periods of glaciation, the species of each echelon coming to differ progressively from their nearest Eurasian relatives and to become progressively adapted to a warmer climate. While these generalizations seem relatively safe, it is more difficult, if not impossible, to deduce the time at which any given species entered our fauna, or even to state which species belong to any specific wave of migration.

The remaining 41% of our species are much more southerly in their general distribution and show few if any affinities to the Eurasian fauna. This group falls readily into two components: those having few or no relatives in Central and South America,

and hence rather uniquely characteristic of the Sonoran subregion of the Nearctic region, and those groups having many representatives in the Neotropical region. The latter group, or *Tropical* element, makes up 25% of our fauna, and may be subdivided into the *tropicopolitan* element and the strictly *neotropical* element. The former includes *Ridestus, Gymnochares, Poecilopompilus, Tachypompilus, Arachnophroctonus, Aporinellus,* and *Paracyphononyx*; these are groups occurring throughout the tropics of the world, which were probably cosmopolitan during the warmer parts of the Tertiary, having later been compressed into the tropics by Pleistocene glaciation. The latter, or *neotropical* element, includes two subgenera of *Anoplius, Notiochares* and *Anopliodes,* groups which apparently developed in South America during its period of separation from North America in the Tertiary, since these groups are strictly Neotropical except for a few species which have invaded the southern parts of North America. As in the Holarctic fauna, one may perceive among the Tropical elements a number of apparent waves of migration, in this case northward. Several species range as far north as Canada, for example, *Anoplius* (*Arachnophroctonus*) *relativus* and *Aporinellus taeniatus,* while others, such as *Anoplius* (*Anopliodes*) *parsonsi,* barely reach the southern extremities of the United States. This is probably not so much an indication of the time of migration as of the degree of adaptive temperature-tolerance attained by these forms during the successive cold periods of the Pleistocene, during which they were alternately compressed into the tropics and allowed to extend their ranges northward.

In many ways the most interesting part of our fauna is the remaining 16%, the apparently endemic *Sonoran* element. To this group belong the following seven genera or subgenera: *Tastiotenia, Chalcochares, Sericopompilus, Hesperopompilus, Xerochares, Perissopompilus,* and *Allochares.* Three of these are monotypic, and all seven together contain only 15 species. It is characteristic of these forms that they have no close relatives either to the south or to the north. Apparently they represent relicts of an earlier fauna which has been able to survive recurrent periods of glaciation and the competition of more highly evolved forms by becoming somewhat localized in the desert regions of the south-

western United States and northern Mexico. The only one of these seven groups which is known to occur outside the Sonoran subregion of the Nearctic region is *Sericopompilus*, which also occurs in Australia. In our fauna the species of *Sericopompilus* are relatively widespread, but their focal point is clearly in the Southwest. The other groups are all known from a few relatively uncommon species which are mostly southwestern in distribution. Certain of these genera, particularly *Tastiotenia* and *Chalcochares*, appear to have many primitive characteristics, as described in the text. It is these relict genera which are of most interest from a phylogenetic standpoint, but unfortunately it is just these groups which are least known at the present time. Next to nothing is known regarding the biology of any of the genera composing this faunal element.

Phylogeny of the Nearctic Genera.—Any discussion of phylogeny based on a limited fauna and without paleontological data is unlikely to yield much in the way of valid conclusions. Nevertheless, I should like to bring together in this section a number of suggestions made in the text regarding the possible relationships of some of our genera. The accompanying chart (Plate XV) presents these suggestions in the form of a phylogenetic tree, which should be regarded as highly tentative. A full-scale consideration of the phylogeny of the Pompilini must await a more thorough understanding of the fauna of several zoogeographic regions and a comprehensive study of the classification of the family as a whole.

Certain of the Sonoran genera mentioned above suggest themselves as possibly close to the ancestral stock of the Pompilini. *Tastiotenia* is known only from the female sex, and must be regarded as of very doubtful phylogenetic position. *Chalcochares* is somewhat better known, and has a number of primitive characteristics, including a rather broad hind wing with an unusually large anal lobe. The rather short legs and antennae and the heavy, hairy body may also be primitive characters, though the reason for considering them so is not altogether clear, unless it is merely that they suggest some of the Scolioidea which may possibly be ancestral to the Pompilidae as a whole. We might envisage our ancestral pompilid ("Ancestor B" in Plate XV) as a primitive scolioid having somewhat the aspect of *Chalcochares*, giving rise

to the subfamily Pepsinae through such a genus as, for example, *Chirodamus,* and to the Pompilinae through *Chalcochares.* The genus *Psorthaspis* (here placed in the Aporini) appears to be related to *Chalcochares,* and may be derived from it. In the Pompilini, some species of *Evagetes,* especially *ingenuus,* have certain characters in common with *Chalcochares,* particularly the slight constrictions between the abdominal segments, the appendiculate submedian cell of the hind wing, the bluish vestiture, short antennae, etc. From *Evagetes,* which possesses a fully developed tarsal comb, the remainder of the tribe can perhaps be accounted for with less difficulty, since both *Agenioideus* and *Hesperopompilus* show some similarities to *Evagetes,* and from these genera in turn a considerable number of other groups may be derived rather logically.

Certain defects in this hypothesis must, however, be pointed out (other than the obvious one that the evidence in favor of it is extremely slim). Although the biology of *Chalcochares* is unknown, both *Evagetes* and *Psorthaspis* have somewhat specialized behavior-patterns, the members of the former group being parasites of other Pompilini, those of the latter group being predators on trap-door spiders. Furthermore, from our ancestral pompilid it is necessary to derive the Ceropalinae, the most distinctive group in the family, which undoubtedly split off very early from the main stock of the Pompilidae. Yet *Ceropales* and its allies appear to have almost nothing in common with *Chalcochares* or with our hypothetical ancestor. Rather than to elaborate upon this theory further, or to abandon it altogether, I should like to suggest an alternate possibility.

Under the discussion of *Agenioideus* in the text (Part I, p. 189), I have suggested several reasons for suspecting that this widely distributed, protean genus may have affinities with the tribe Auplopodini in the Pepsinae. The species of *Agenioideus* are typical spider-hunters, nesting in the ground or in niches of various sorts, as we might imagine our ancestral pompiline did. Although many of the Auplopodini build mud nests, others appear to nest in niches much as do the members of the subgenus *Gymnochares* of the genus *Agenioideus.* There is also the interesting Neotropical genus *Priochilus,* which uses leaf fragments

in constructing its nest, and which morphologically seems to be somewhat intermediate between the Pompilinae and the Pepsinae. The genus *Tastiotenia* might be accounted for as a relict of an early pompiline auplopodine type. Not only might the Ceropalinae be more easily derived from such a stock, but certain genera usually placed in the Auplopodini have recently been transferred by Townes [28] to the Ceropalinae, indicating perhaps that there is no great morphological gulf between these two groups.

If we accept the hypothesis that *Agenioideus* is allied to the Auplopodini and more or less ancestral to the remainder of the Pompilini, it is logical to conclude that the ancestral pompilid ("Ancestor A" in Plate XV) was a slender, long-legged, smooth-bodied insect, not at all like "Ancestor B" and probably more like a rhopalosomatid than a scolioid. Indeed, Arnold [29] and Reid [30] have included in the Pompilidae certain genera which are almost certainly Rhopalosomatidae. Curiously, Reid compares one of these genera, *Olixon*, to *Homonotus*, one of the most highly evolved of the Pompilidae, when in all probability it is related to the ancestral stock of this family. The similarity of the male genitalia of *Olixon* to those of *Rhopalosoma* was noted long ago. The genitalia of *Homonotus* have almost nothing in common with those of *Olixon*, although the genitalia of *Ceropales* are in some ways more similar to those of *Olixon* than to those of most Pompilidae. To derive the Pompilidae from the Rhopalosomatidae is, however, of little help in relating the pompilids to other Aculeata, since the rhopalosomatids are themselves a decidedly isolated group, perhaps derived from some primitive bethyloid type.

In any event, it ultimately makes relatively little difference within the tribe Pompilini whether we start from ancestor A and *Agenioideus* or ancestor B and *Evagetes*. These are both

[28] Townes, H. K., 1951, U. S. Dept. Agri., Monogr. 2, p. 919. Townes transfers *Minagenia* to the Ceropalinae. While I am not sure that I entirely agree with Townes in this placement of *Minagenia*, at least his action illustrates the point in question.

[29] Arnold, G., 1935, Ann. Transvaal Mus., 15: 471-483. [Genus *Psyllosphex* Arnold.]

[30] Reid, J. A., 1939, Proc. Royal Ent. Soc. London (B) 8: 95-102.

relatively unspecialized genera, and they share certain characteristics in common, such as the poorly developed pulvillar pad and comb, dentate claws throughout, etc. It seems likely that they are in some way related, and either might conceivably have been derived from the other. From *Agenioideus* probably was derived the rather similar *Sericopompilus,* and from this genus in turn the two epeirid-hunting genera *Episyron* and *Poecilopompilus;* these three genera form a closely-knit generic complex, having several characteristics in common, as described under *Sericopompilus* in the text (Part I, p. 202).

Forming another line of ascent, either by way of *Agenioideus* or *Evagetes,* is a group of genera and subgenera which may collectively be called the *Pompilus*-complex. *Hesperopompilus* appears to have a number of characters in common with both *Evagetes* and *Agenioideus,* such as the poorly developed pulvillar comb, the frequently bluish vestiture, short antennae in the males, slender appendages and delicate build of the body, etc. *Hesperopompilus* and *Pompilus s. str.* agree in a number of characters, most noteworthy of which are the peculiar tufts at the base of the male subgenital plate. This character is shared by the genus *Aporinellus,* which is probably a specialized offshoot of this same stock. From *Hesperopompilus* may also be derived the other subgenera of *Pompilus,* culminating in *Anoplochares,* which has lost the tarsal comb and become somewhat specialized in its behavior-patterns.

The largest and most successful offshoot of the *Pompilus*-complex is the large genus *Anoplius* with its numerous subgenera. Of these, *Arachnophroctonus* appears to be most generalized and most *Pompilus*-like, and may have served as the stock from which the other subgenera arose. One subgenus, *Anoplius s. str.,* has lost the tarsal comb, and some of the species have acquired rather specialized habits. *Anoplius s. lat.* is one of the largest genera of the entire family in the Americas, having probably over 100 species in North and South America. *Tachypompilus* is a cosmopolitan genus of uncertain origins, but the bifid claws of the male suggest a possible relationship to *Anoplius.*

The position of the genus *Allochares* is very uncertain. It seems to have been derived from some early *Pompilus*-like stock, and

may possibly be a relict of the stock which gave rise to the Old World genus *Homonotus* and its allies, since it shows some resemblances to that group. The genus *Paracyphononyx* is also uncertain in position. The superficial resemblance of this genus to *Notocyphus* leads me to suspect that it may exhibit convergence in structure and in habits to that genus, which is known to attack certain spiders in their nests and oviposit upon them *in situ*. Nothing is actually known of the biology of either *Paracyphononyx* or *Allochares*. Indeed, we know so little about the biology of so many critical groups in the Pompilidae that I venture to suggest that more can now be learned about the phylogeny of this family from field studies than from further analysis of the comparative external structure of these wasps.

The foregoing discussion, for the sake of brevity, is not fully documented as to the reasons behind many of the supposed relationships. In most cases, these reasons are discussed under the various genera and subgenera in the text. The highly tentative nature of these phylogenetic conclusions cannot be stated too forcibly. If it be argued that my phylogenetic tree is an exceedingly weak one and apt to be blown over in an early storm (which I admit)—then at least I have provided two trunks for its better support!

Explanation of Figures

Note: In all figures of male genitalia, the ventral aspect is shown on the left half of the figure, the dorsal aspect on the right. Numbering of the figures is continuous from Parts I and II of this study.

Plate VI

Fig. 171.—*Pompilus* (*Pompilus*) *plumbeus* (Fabricius), male genitalia.
Fig. 172.—*P.* (*Xerochares*) *expulsus* Schulz, male genitalia.
Fig. 173.—*P.* (*Hesperopompilus*) *jacintoensis* Evans, male genitalia.
Fig. 174.—*P.* (*H.*) *orophilus* Evans, male genitalia.
Fig. 175.—*P.* (*H.*) *evagetoides* new species, male genitalia.
Fig. 176.—*P.* (*H.*) *boharti* new species, male genitalia.

Plate VII

Fig. 177.—*P.* (*Perissopompilus*) *phoenix* Evans, male genitalia.
Fig. 178.—*P.* (*P.*) *phoenix* Evans, sixth abdominal sternite of male.
Fig. 179.—*P.* (*Ammosphex*) *parvulus* (Banks), male genitalia.
Fig. 180.—*P.* (*A.*) *anomalus* (Dreisbach), male genitalia.
Fig. 181.—*P.* (*A.*) *angularis* (Banks), male genitalia.
Fig. 182.—*P.* (*A.*) *imbecillus* (Banks), male genitalia.

Plate VIII

Fig. 183.—*P.* (*A.*) *solonus solonus* (Banks), male genitalia.
Fig. 184.—*P.* (*A.*) *solonus silvivagus* new subspecies, male genitalia.
Fig. 185.—*P.* (*A.*) *michiganensis michiganensis* (Dreisbach), male genitalia.
Fig. 186.—*P.* (*A.*) *michiganensis dakota* (Dreisbach), male genitalia.
Fig. 187.—*P.* (*A.*) *occidentalis* (Dreisbach), male genitalia.
Fig. 188.—*P.* (*A.*) *luctuosus* Cresson, male genitalia.

Plate IX

Fig. 189.—*P.* (*Arachnospila*) *fumipennis* Zetterstedt, male genitalia.
Fig. 190.—*P.* (*A.*) *scelestus* Cresson, male genitalia.
Fig. 191.—*P.* (*A.*) *arctus* Cresson, male genitalia.
Fig. 192.—*P.* (*Anoplochares*) *apicatus* Provancher, male genitalia.
Fig. 193.—*Allochares azureus* (Cresson), male genitalia.
Fig. 194.—*Paracyphononyx funereus* (Lepeletier), male genitalia.

Plate X

Fig. 195.—*Aporinellus taeniatus* (Kohl), male genitalia.
Fig. 196.—*A. fasciatus* (Smith), male genitalia.
Fig. 197.—*A. bridwelli* new species, male genitalia.
Fig. 198.—*A. completus* Banks, male genitalia.
Fig. 199.—*A. sinuatus* new species, male genitalia.
Fig. 200.—*A. apicatus* (Banks), male genitalia.

Plate XI

Fig. 201.—*Pompilus* (*Pompilus*) *plumbeus* (Fabricius), male subgenital plate.
Fig. 202.—*P.* (*Hesperopompilus*) *jacintoensis* Evans, male subgenital plate.
Fig. 203.—*P.* (*H.*) *orophilus* Evans, male subgenital plate.
Fig. 204.—*P.* (*H.*) *boharti* new species, male subgenital plate.
Fig. 205.—*P.* (*H.*) *evagetoides* new species, male subgenital plate.
Fig. 206.—*P.* (*Xerochares*) *expulsus* Schulz, male subgenital plate.
Fig. 207.—*P.* (*Perissopompilus*) *phoenix* Evans, male subgenital plate.
Fig. 208.—*P.* (*Ammosphex*) *angularis* (Banks), male subgenital plate.
Fig. 209.—*P.* (*A.*) *parvulus* (Banks), male subgenital plate.
Fig. 210.—*P.* (*A.*) *anomalus* (Dreisbach), male subgenital plate.
Fig. 211.—*P.* (*A.*) *michiganensis michiganensis* (Dreisbach), male subgenital plate.
Fig. 212.—*P.* (*A.*) *michiganensis dakota* (Dreisbach), male subgenital plate.

Plate XII

Fig. 213.—*P.* (*A.*) *imbecillus* (Banks), apex of male abdomen.
Fig. 214.—*P.* (*A.*) *michiganensis michiganensis* (Dreisbach), apex of male abdomen.
Fig. 215.—*P.* (*A.*) *luctuosus* Cresson, apex of male abdomen.
Fig. 216.—*P.* (*A.*) *occidentalis* (Dreisbach), apex of male abdomen.
Fig. 217.—*P.* (*A.*) *solonus solonus* (Banks), apex of male abdomen.
Fig. 218.—*P.* (*A.*) *solonus silvicolens* new subspecies, apex of male abdomen.
Fig. 219.—*P.* (*Arachnospila*) *scelestus* Cresson, apex of male abdomen.
Fig. 220.—*P.* (*A.*) *fumipennis* Zetterstedt, apex of male abdomen.
Fig. 221.—*P.* (*A.*) *arctus* Cresson, apex of male abdomen.
Fig. 222.—*P.* (*Anoplochares*) *apicatus* Provancher, apex of male abdomen.
Fig. 223.—*P.* (*A.*) *similaris* (Banks), male subgenital plate.
Fig. 224.—*P.* (*Ammosphex*) *luctuosus* Cresson, hind basitarsus and tibial spurs of female.
Fig. 225.—*P.* (*A.*) *occidentalis* (Dreisbach), hind basitarsus and tibial spurs of female.
Fig. 226.—*P.* (*Pompilus*) *plumbeus* (Fabricius), inner side of last segment of front tarsus of male.
Fig. 227.—*P.* (*Hesperopompilus*) *jacintoensis* Evans, inner side of last segment of front tarsus of male.
Fig. 228.—*P.* (*Xerochares*) *expulsus* Schulz, inner side of last segment of front tarsus of male.
Fig. 229.—*P.* (*Ammosphex*) *michiganensis* (Dreisbach), inner side of last segment of front tarsus of male.
Fig. 230.—*P.* (*Arachnospila*) *arctus* Cresson, inner side of last segment of front tarsus of male.
Fig. 231.—*P.* (*Anoplochares*) *apicatus* Provancher, upper side of last segment of front tarsus of male.
Fig. 232.—*P.* (*Arachnospila*) *scelestus* Cresson, last segment of hind tarsus of female.
Fig. 233.—*P.* (*Ammosphex*) *michiganensis* (Dreisbach), clypeus of female.
Fig. 234.—*P.* (*A.*) *anomalus* (Dreisbach), clypeus of female.
Fig. 235.—*P.* (*A.*) *imbecillus* (Banks), clypeus of female.
Fig. 236.—*P.* (*A.*) *luctuosus* Cresson, clypeus of female.

Plate XIII

Fig. 237.—*P.* (*Perissopompilus*) *phoenix* Evans, wings.
Fig. 238.—*P.* (*P.*) *perfasciatus* new species, wings.
Fig. 239.—*P.* (*Ammosphex*) *solonus* (Banks), wings.
Fig. 240.—*P.* (*A.*) *michiganensis* (Dreisbach), wings.
Fig. 241.—*P.* (*Arachnospila*) *scelestus* Cresson, wings.
Fig. 242.—*P.* (*Anoplochares*) *similaris* (Banks), marginal and second and third submarginal cells of fore wing.

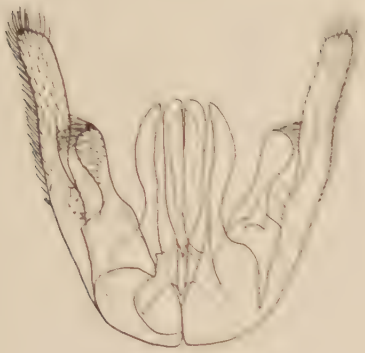
Fig. 243.—*Aporinellus fasciatus* (Smith), marginal and second and third submarginal cells of specimen having three submarginal cells.
Fig. 244.—*A. fasciatus* (Smith), wings of a specimen having only two submarginal cells.
Fig. 245.—*A. taeniatus* (Kohl), marginal and second submarginal cells of fore wing.
Fig. 246.—*A. sinuatus* new species, marginal and second submarginal cells of fore wing.
Fig. 247.—*Paracyphononyx funereus* (Lepeletier), wings.
Fig. 248.—*P. funereus* (Lepeletier), antenna of male.
Fig. 249.—*P. funereus* (Lepeletier), male subgenital plate.

Plate XIV

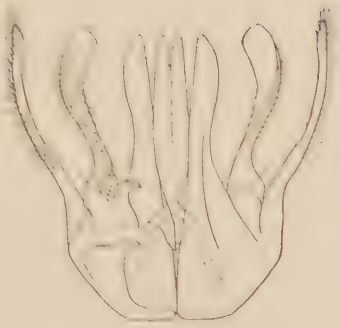
Fig. 250.—*Aporinellus sinuatus* new species, head of female.
Fig. 251.—*A. completus* Banks, head of female.
Fig. 252.—*A. fasciatus* (Smith), head of female.
Fig. 253.—*A. sinuatus* new species, dorsal view of head and antenna of male.
Fig. 254.—*A. apicatus* (Banks), basal five segments of antenna of male.
Fig. 255.—*A. taeniatus* (Kohl), apical segment of hind tarsus of female.
Fig. 256.—*A. sinuatus* new species, antenna of female.
Fig. 257.—*A. apicatus* (Banks), antenna of female.
Fig. 258.—*A. fasciatus* (Smith), lateral view of propodeum of female.
Fig. 259.—*A. fasciatus* (Smith), apical margin of sixth abdominal sternite of male.
Fig. 260.—*A. completus* Banks, apical margin of sixth abdominal sternite of male.
Fig. 261.—*A. apicatus* (Banks), lateral view of propodeum of female.
Fig. 262.—*A. taeniatus* (Kohl), male subgenital plate.
Fig. 263.—*A. completus* Banks, male subgenital plate.
Fig. 264.—*A. fasciatus* (Smith), male subgenital plate.
Fig. 265.—*A. bridwelli* new species, male subgenital plate.

Plate XV

Chart suggesting possible relationships and phylogeny of the Nearctic genera of Pompilini. The line of dashes leading from Ancestor "A" represents one possible origin of the tribe; the dash-dot line leading from Ancestor "B" represents an entirely different theory of origin. These two types of lines should therefore be read separately, and not simultaneously. Solid lines apply to either theory.

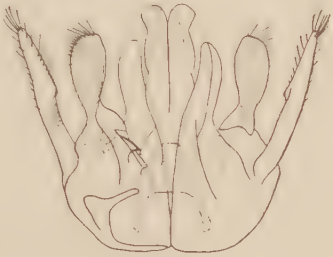


171 POMPILUS PLUMBEUS



172. P. EXPULSUS

173. P. JACINTOENSIS



174. P. OROPHILUS

175. P. EVAGETOIDES

176. P. BOHARTI

EVANS—NEARCTIC SPIDER WASPS

177 POMPILUS PHOENIX

178 P. PHOENIX

179. P. PARVULUS

180 P. ANOMALUS

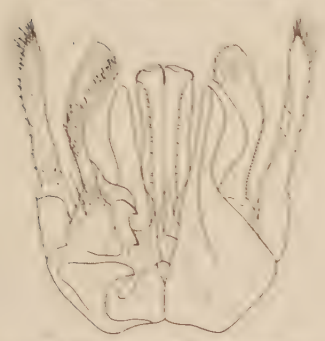
181. P. ANGULARIS

182. P. IMBECILLUS

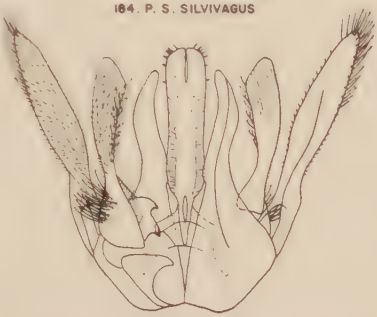
EVANS—NEARCTIC SPIDER WASPS

183. POMPILUS SOLONUS SOLONUS

184. P. S. SILVIVAGUS



185. P. MICHIGANENSIS MICHIGANENSIS



186. P. M. DAKOTA

187. P. OCCIDENTALIS

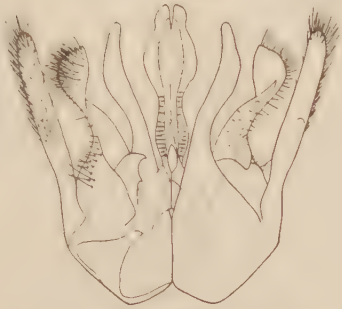
188. P. LUCTUOSUS

EVANS—NEARCTIC SPIDER WASPS

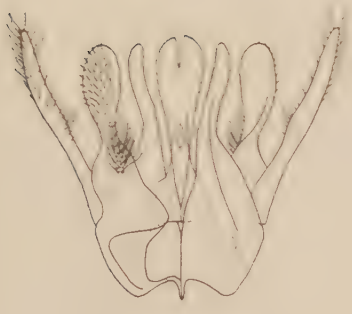
189 POMPILUS FUMIPENNIS

190 P SCELESTUS

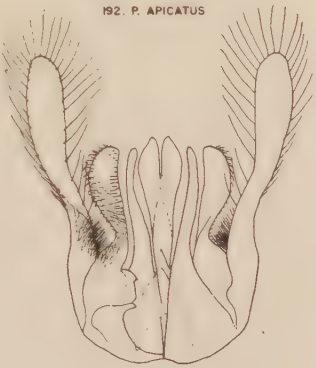
191 P ARCTUS



192. P. APICATUS



193. ALLOCHARES AZUREUS



194. PARACYPHONONYX FUNEREUS

EVANS—NEARCTIC SPIDER WASPS

195. APORINELLUS TAENIATUS

196. A. FASCIATUS

197. A. BRIDWELLI

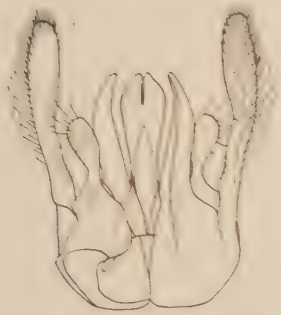
198. A. COMPLETUS

199. A. SINUATUS

200. A. APICATUS

195. APORINELLUS TAENIATUS

196 A FASCIATUS

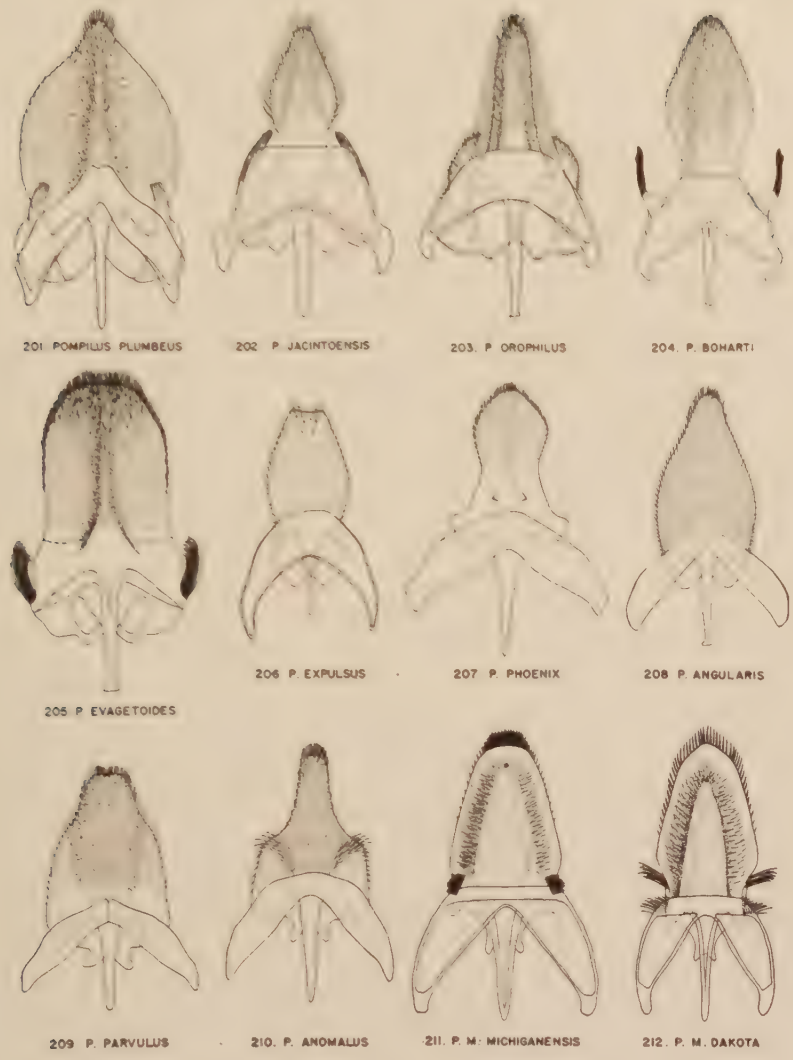


197. A. BRIDWELLI

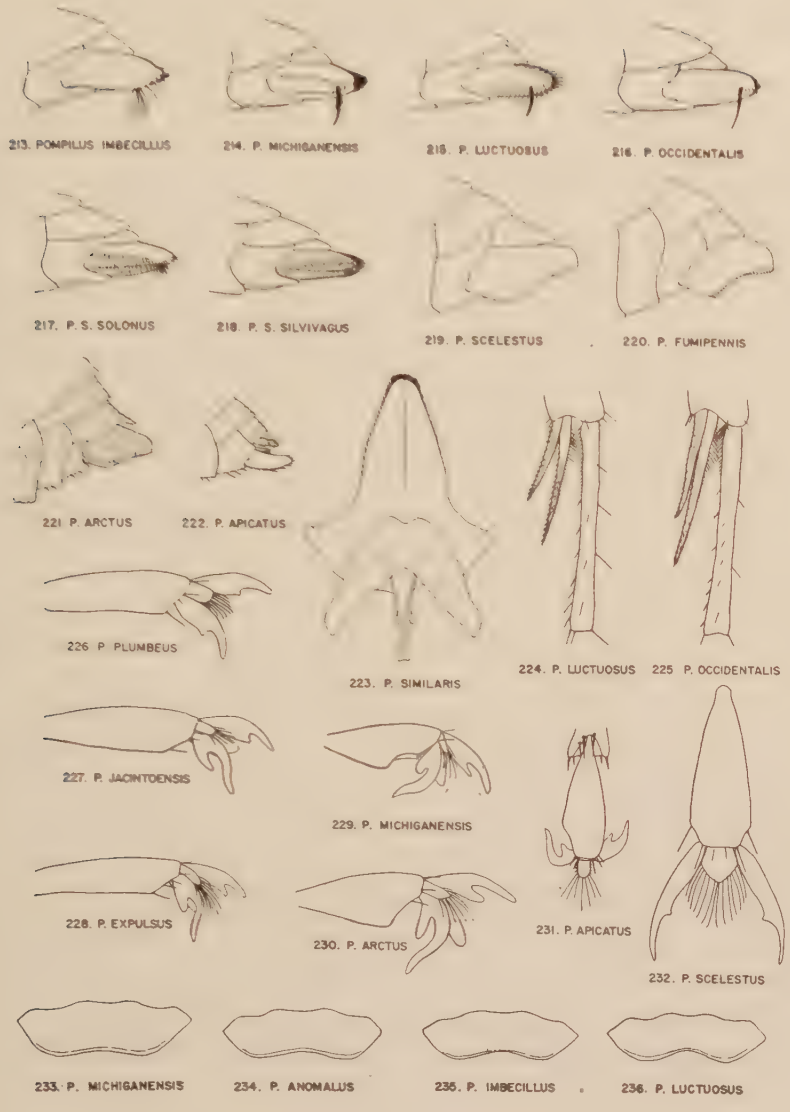
198. A. COMPLETUS

199. A. SINUATUS

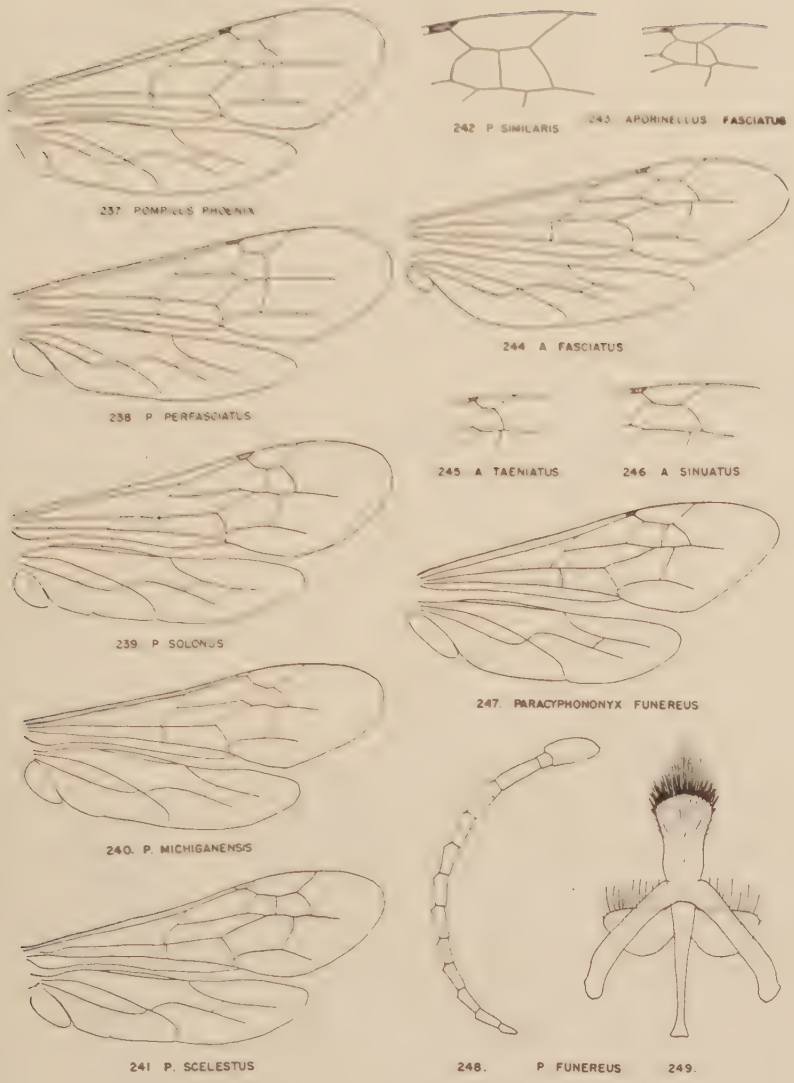
200. A. APICATUS



EVANS—NEARCTIC SPIDER WASPS



EVANS—NEARCTIC SPIDER WASPS

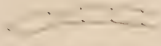


EVANS—NEARCTIC SPIDER WASPS

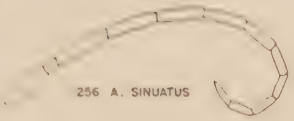
250. APORINELLUS SINUATUS

251. A. COMPLETUS

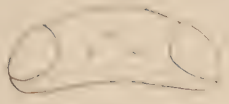
252. A. FASCIATUS



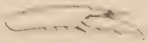
254. A. APICATUS



256. A. SINUATUS



253. A. SINUATUS



255. A. TAENIATUS

257. A. APICATUS

259. A. FASCIATUS

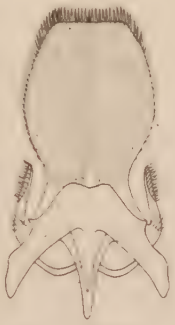
258. A. FASCIATUS

260. A. COMPLETUS

261. A. APICATUS

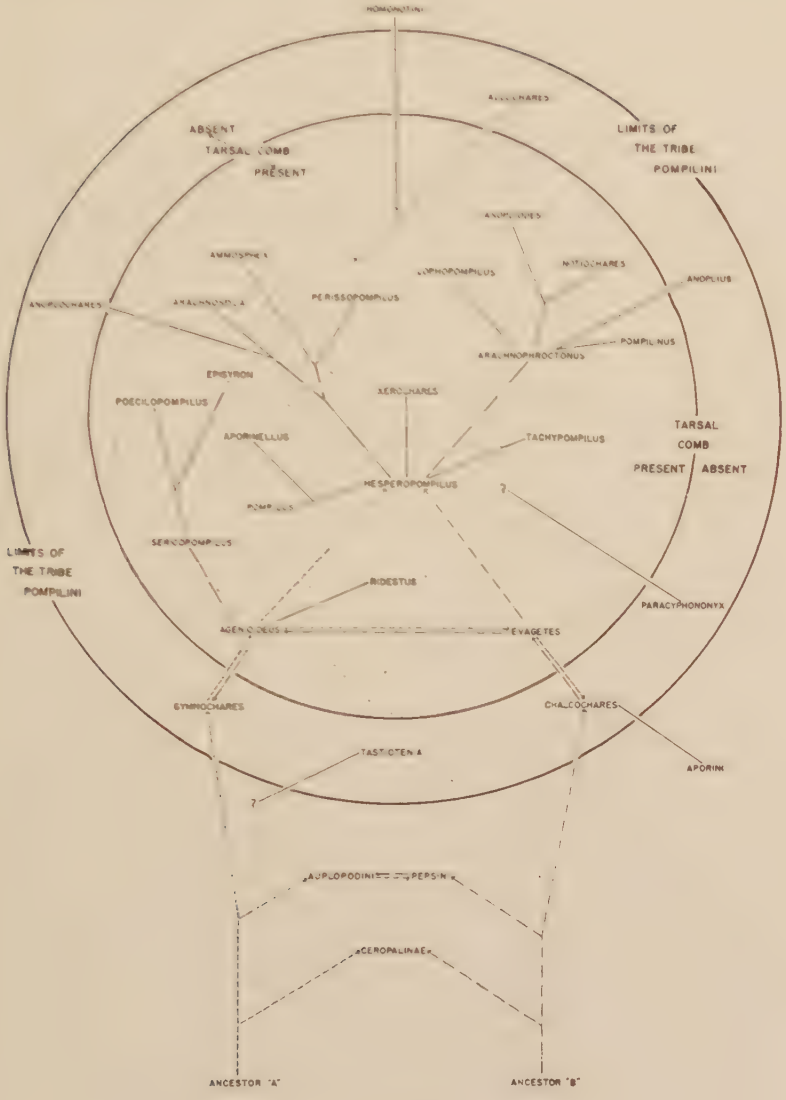
262. A. TAENIATUS

263. A. COMPLETUS



264. A. FASCIATUS

265. A. BRIDWELLI



EVANS—NEARCTIC SPIDER WASPS

CHECK-LIST

The following is a listing of the genera and species of Nearctic Pompilini in the order in which they were considered in this study. The same numbering is used, and references to the volume and pages of the Transactions on which each was described or discussed are included.

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10. *insolens* (Banks), 1912. 76: 304-306.
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4. *fulgidus* (Cresson), 1865. 76: 339-341.
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5. *evagetoides* Evans, 1951. 77: 217-218.
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2. *perfasciatus* Evans, 1951. 77: 225-226.
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1. *funereus* (Lepeletier), 1845. 77: 306-308.

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